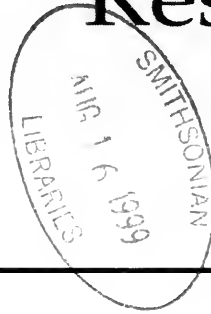




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A Review of the North American Species of *Thinodytes* Graham and *Mauleus* Graham (Hymenoptera: Pteromalidae)

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Abstract.—The *Halticoptera*-group is defined as containing those pteromaline pteromalid genera with a reticulate body, acarinate pronotal collar, weakly developed notauli, weakly delimited frenum, propodeum with the median carina and plicae connected posteriorly by a W-shaped carina, petiole with a basal flange, and the hind margin of the first gastral tergite sinuous laterally and usually emarginate medially. Genera included in this group are *Halticoptera* Spinola, *Halticopterina* Erdős, *Andersena* Bouček, *Thinodytes* Graham, *Syntomopus* Walker, *Mauleus* Graham, and *Ploskana* Bouček. *Thinodytes* and *Mauleus* are revised for the Nearctic region and keys to the world's described species are given. New species include *T. caroticus* n. sp., *T. cyzicopsis* n. sp., *T. petiolatus* n. sp., *M. cultratus* n. sp., *M. iligneus* n. sp., and *M. venetus* n. sp. *Polycystus nigritus* Howard is transferred to *Mauleus* as *M. nigritus* n. comb. and *Gastrancistrus cephalon* Walker is transferred to *Thinodytes* as *T. cephalon* n. comb. *Bubekia fallax* Gahan n. syn. is synonymized with *T. cephalon* Walker.

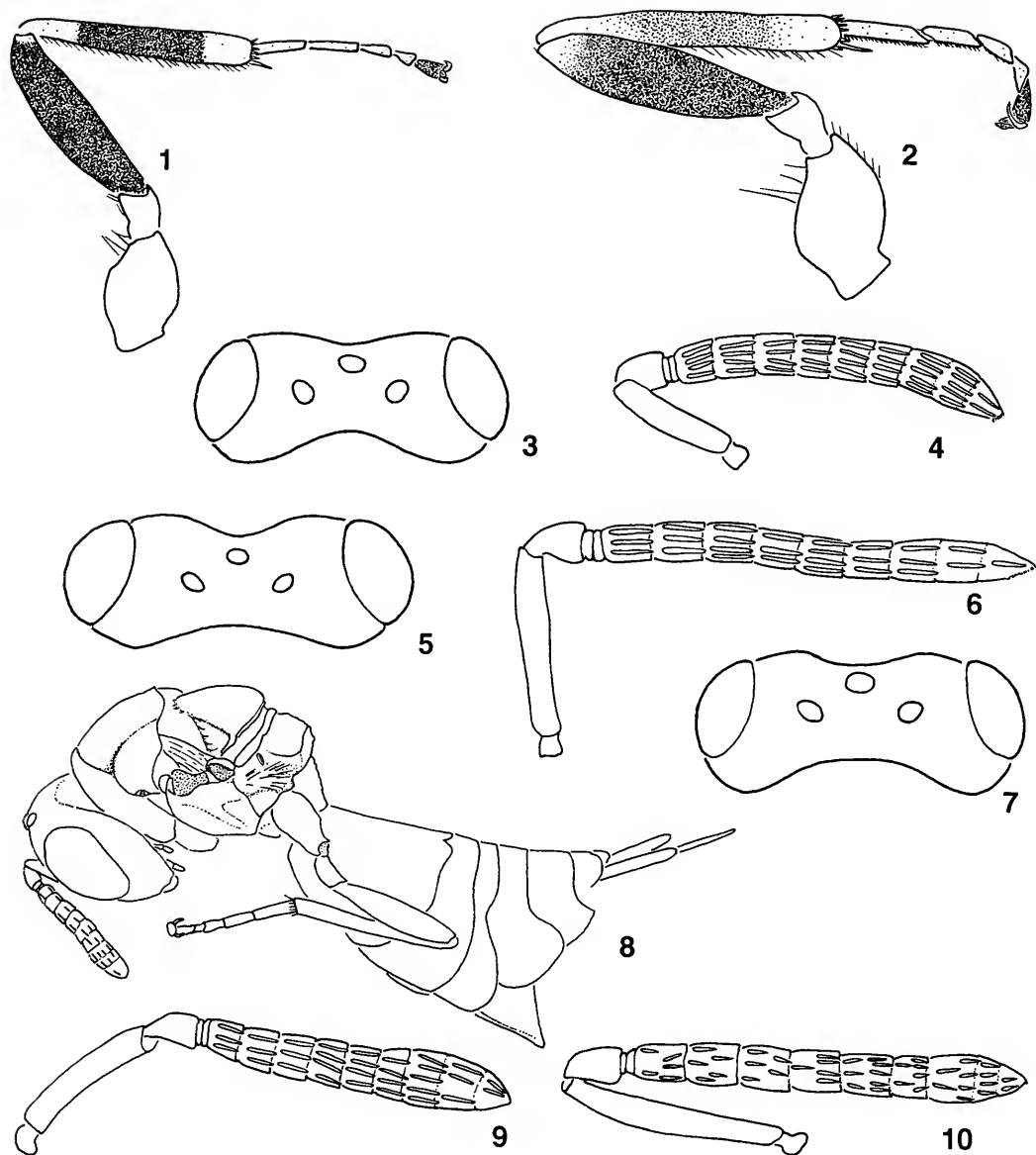
INTRODUCTION

The *Halticoptera*-group is herein defined as containing those pteromaline pteromalid genera with: body reticulately sculptured, pronotal collar acarinate (Figs 21, 22), notauli weakly developed (Figs 21, 22), frenum weakly delimited (Figs 21, 22), propodeum with a sharp median carina and the plicae connected posteriorly by a W-shaped carina (Figs 17–20), petiole braced basally by an anteriorly directed lateral and ventral flange (Figs 17–20), and hind margin of first gastral tergite sinuous laterally and usually emarginate medially (Figs 21, 22). Genera of this group include *Halticoptera* Spinola, *Halticopterina* Erdős, *Andersena* Bouček, *Thinodytes* Graham, *Syntomopus* Walker, *Ploskana* Bouček, and *Mauleus* Graham. Three other genera that show many of the characteristics of the *Halticoptera*-group and which probably are more or less closely related to the *Halticoptera*-group

are *Notoglyptus* Masi, *Sphegigaster* Spinola, and *Schimitschekia* Bouček.

Except for *Thinodytes* and *Mauleus*, the North American species of all the genera of the *Halticoptera*-group occurring in the Nearctic region were recently reviewed or are currently being studied. *Andersena* includes only one species (Bouček 1993). Anderson (1990) reviewed *Halticopterina* for North America and is currently revising *Halticoptera*. The world species of *Notoglyptus* and the Nearctic species of *Syntomopus* and *Sphegigaster* were reviewed by Heydon (1988), Heydon (1993), and Heydon and LaBerge (1988), respectively. This paper reviews the Holarctic species of *Thinodytes* and *Mauleus*. [*Ploskana* was reviewed by Bouček (1976).] Research by the author has revealed the presence of numerous species of both these genera in Central and South America.

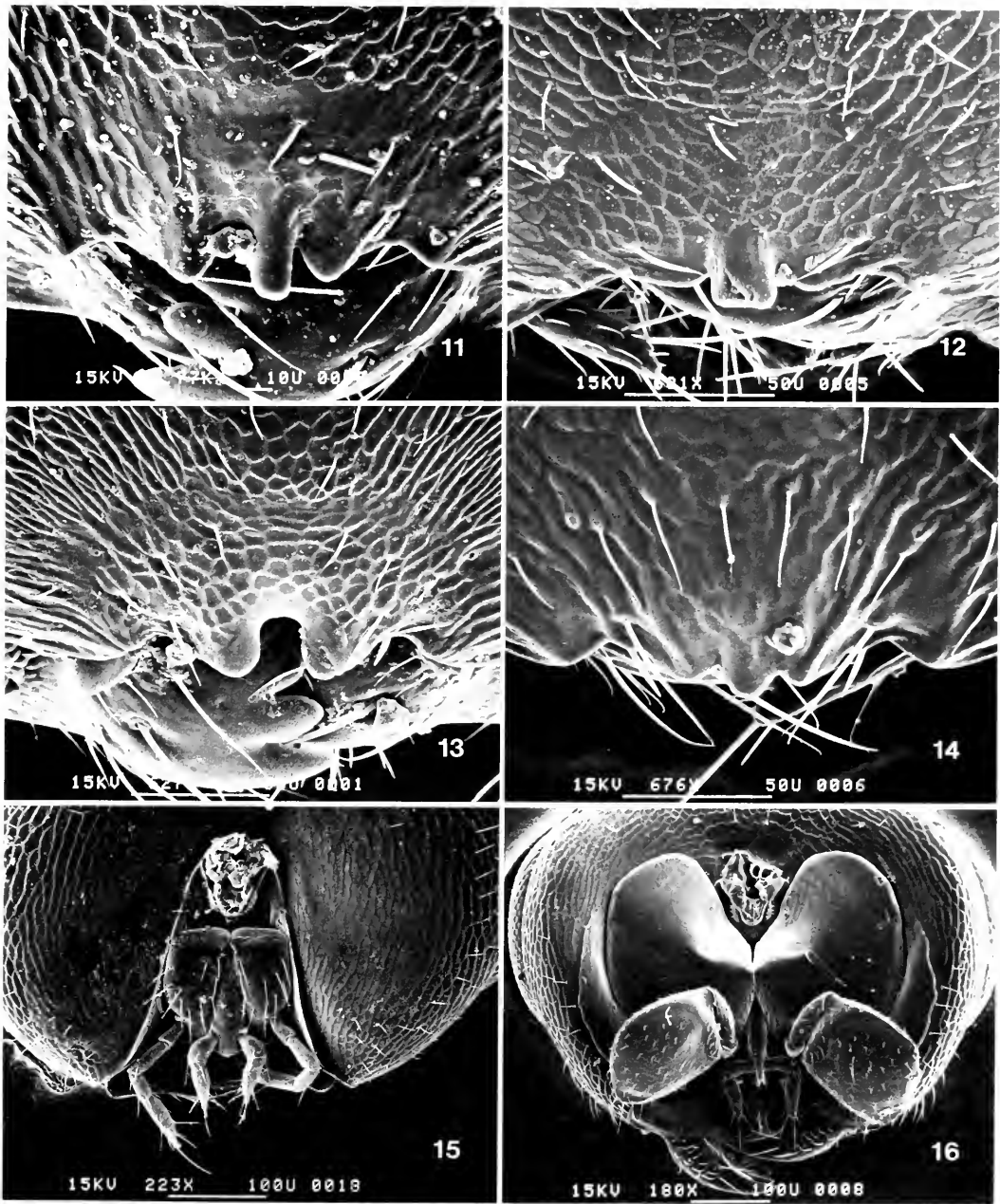
Thinodytes previously contained two described species, the Palearctic species *T. cyzicus* (Walker) 1839, and the Carib-



Figs. 1–10. 1, *Thinodytes caroticus* n. sp., female hind leg; 2, *Thinodytes cephalon* (Walker), 2, female hind leg; 3, 4, *Thinodytes cyzicopsis* n. sp., female head dorsal view, 4, male antenna; 5, 6, *Thinodytes petiolatus* n. sp., 5, female head dorsal view, 6, male antenna; 7, *Thinodytes cyzicus* n. sp., female head dorsal view; 8, *Mauleus cultratus* n. sp., female habitus; 9, *Mauleus iligneus* n. sp., female antenna; 10, *Mauleus venetus* n. sp., female antenna.

bean species *T. clypeatus* (Girault) 1918. To these I add the New World species *T. cephalon* (Walker) 1843, **n. comb.**, and describe four new Nearctic species—*T. caroticus* n. sp., *T. cyzicopsis* n. sp., *T. petiolatus* n. sp., and *T. santerna* n. sp. *Mauleus*

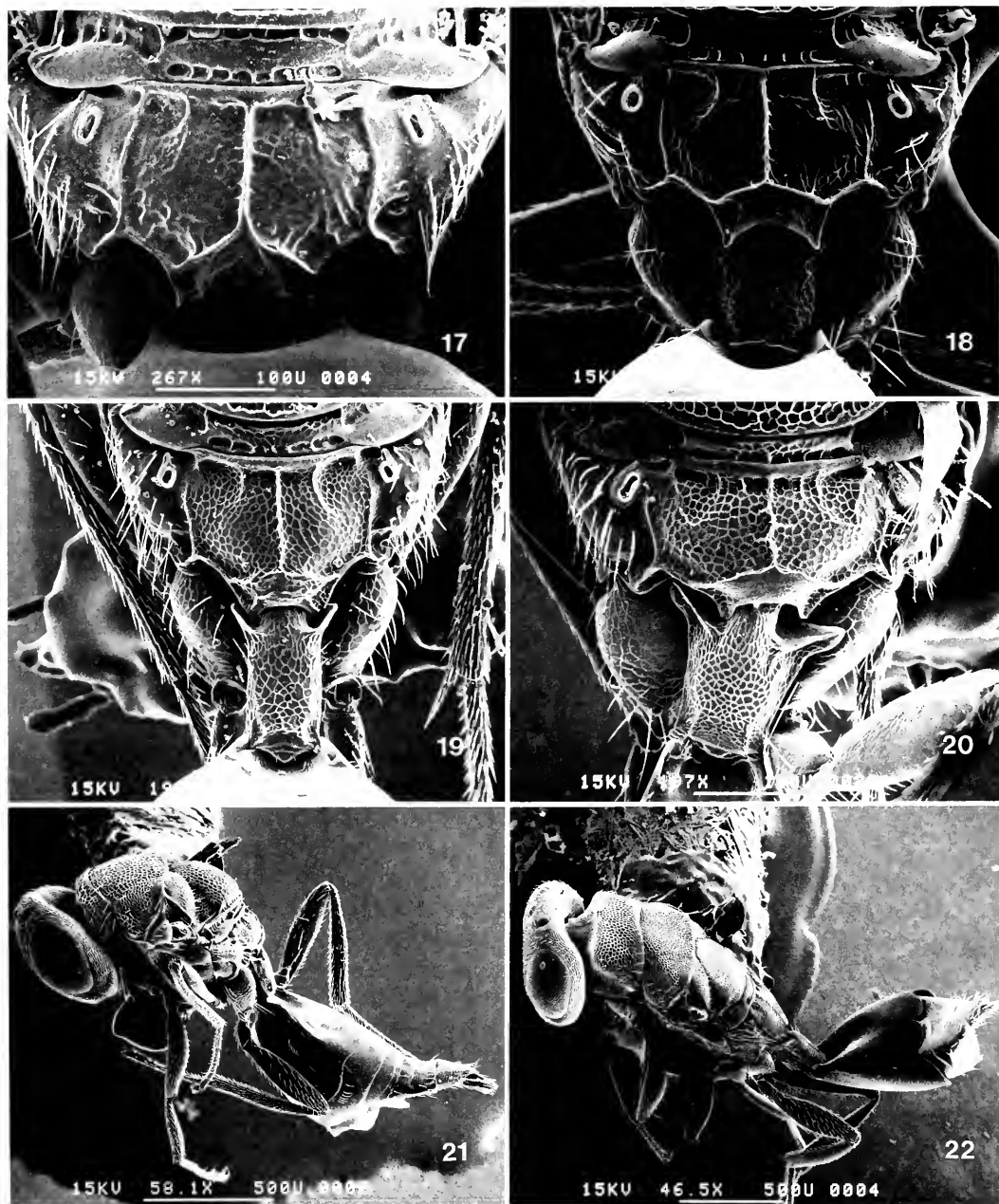
was created for the species *M. maderensis* Graham, 1981 from Madeira. However, this species is associated with plants native to Mexico and is suspected to be native to the New World (Bouček and Rasplus 1991). The New World origin of this



Figs. 11–16. 11, *Thinodytes petiolatus* n. sp., female clypeus; 12, *Thinodytes cephalon* (Walker), female clypeus; 13, *Mauleus iligneus* n. sp., male clypeus; 14, *Syntomopus americanus* Ashmead, female head dorsal view; 15, *Mauleus iligneus* n. sp., male head posterior aspect; 16, *Halticoptera* sp., male head posterior aspect.

species is given more credence by the presence of a described Neotropical *Mauleus* species, *M. nigratus* (Howard), 1897 **n. comb.** and the author's discovery of three

new Nearctic species—*M. cultratus* **n. sp.**, *M. iligneus* **n. sp.**, and *M. venetus* **n. sp.** These three new species are described herein.



Figs. 17–22. 17, *Thinodytes cephalon* (Walker), female propodeum and petiole; 18, *Thinodytes cyzicopsis* n. sp., male propodeum and petiole; 19, *Thinodytes petiolatus* n. sp., female propodeum and petiole; 20, 21, *Maudius iligneus* n. sp., 20, male propodeum and petiole, 21, female habitus; 22, *Syntomopus arpedes* Heydon, female habitus.

METHODS

Terminology generally follows that of Graham (1969), except that genal concavity is used instead of genal hollow and

club is used instead of clava. In addition, the gastral tergites are numbered T1–T7 beginning with the first tergite after the petiole. The following abbreviations are used:

the median ocellar diameter is MOD, the ocellar-ocular distance is OOL, the posterior ocellar distance is POL, the lateral ocellar distance is LOL, the multiporous plate sensilla are MPP sensilla, the lower ocular line is LOcL, and the antennal funicular segments are F1 through F6. The measurements given in the descriptions can be converted to millimeters by multiplying by 0.02. The acronyms for the museums from which material was borrowed are listed in the acknowledgments section.

Thinodytes Graham

Dicyclus Thomson, 1876:221, 253. Type species: *Miscogaster cyzicus* Walker, 1839:200; by monotypy (examined). New name needed because of *Dicyclus* Walker, 1833:371, 455.

Thinodytes Graham, 1956:261. Type species: *Miscogaster cyzicus* Walker, 1839:200; by original designation (examined). Peck, Bouček, and Hoffer, 1964:41. Graham, 1969:150, 167. Hedqvist, 1975:167. Dzhanokmen, 1978:82. Bouček and Rasplus, 1991:32.

Description.—Body color varying from almost wholly black to metallic green; scape metallic or nonmetallic. Head and mesosoma mostly alveolate except sculpturing sometimes smooth on frenum (*T. cyzicopsis*, *T. petiolatus*, and *T. santerna*) and median panels of propodeum (*T. santerna*); petiole alveolate in species with quadrate to elongate petiole (Figs 18–20), smooth in species with transverse petiole (Fig. 17); gastral tergites nearly smooth. Clypeus variable, with either three asymmetrically arranged denticles (Fig. 11) (*T. cyzicopsis*, *T. cyzicus*, *T. petiolatus*), three symmetrically arranged denticles (*T. santerna* and *T. clypeatus*) or with single broad asymmetrically placed denticle (Fig. 12) (*T. cephalon* and *T. caroticus*). Head with short genal concavity often present; antennal torulus above LOcL. Antenna with formula 1:1:2:6:3; scape cylindrical, slender; length of flagellum plus pedicel of female less than head width (subequal in length in *T. cyzicopsis*), equal to or slightly greater than head width in male; funicular seg-

ments cylindrical; MPP sensilla usually in single row, their length about equal to length of funicular segment (Figs 4, 6); female club simple apically and with small patch of micropilosity on ventral side of terminal segment, except *T. cephalon* with terminal spine and large patch of micropilosity. Male maxilla with stipites unenlarged; palps slender (Fig. 15). Mesosoma arched dorsally; pronotum with collar very short medially, anterior edge rounded; mesoscutum with notaulus incomplete or extending to hind margin of mesoscutum as impressed line; scutellum as long as wide, lacking anterior median sulcus, with two or three pairs of lateral setae (except *T. santerna* with many pairs), frenum not set off by sulcus; dorsellum a short transverse ridge; propodeum with width of median panels about 1.6× their length (Figs 17–19), plicae and median carina distinct and connected posteriorly by W-shaped carina (Figs 17–19), basal fovea sometimes bordered mesally by short straight carina (Fig. 17) (*T. clypeatus*, *T. cyzicopsis*, and *T. cephalon*), or by long sinuous carina (Figs 18, 19) (*T. cyzicopsis*, *T. cyzicus*, and *T. petiolatus*); spiracles ovate. Fore wing with postmarginal vein about as long as marginal vein but postmarginal vein sometimes distinctly shorter (*T. caroticus* and *T. cephalon*); stigma small, but its height half the distance between stigma and anterior wing margin in *T. clypeatus*; costal cell with one complete and two or three partial distal setal rows; basal cell bare except sometimes a few setae distally (*T. clypeatus* and *T. cyzicus*); basal vein setose except in *T. cephalon*; speculum developed and open posteriorly. Petiole braced basally by lateral and ventral anteriorly directed lamellate flange (Figs 17–19); petiole variable, sometimes transverse, unsclerotized ventrally, and without lateral setae (Fig. 17) (*T. caroticus*, *T. cephalon*, and *T. santerna*), or quadrate to elongate and sclerotized ventrally (*T. clypeatus*, *T. cyzicopsis*, *T. cyzicus*, and *T. petiolatus*); lateral setae sometimes present

(Fig. 19) (*T. cyzicopsis* and *T. petiolatus*); weak median carina present in *T. clypeatus*. Gaster of female ovate, acuminate apically, 1.4–1.8× as long as wide; hypopygium extending $\frac{1}{2}$ to $\frac{2}{3}$ gastral length; hind margin of T1 sinuous laterally and emarginate or straight medially.

Discussion.—Giving a few characters to separate *Thinodytes* from the other genera of the *Halticoptera*-group, particularly *Halticoptera*, *Mauleus*, and *Syntomopus*, is impossible because *Thinodytes* is what is left when the more distinct genera of the *Halticoptera*-group are characterized. Apomorphic characters among related genera common to all *Thinodytes* species such as the reticulate body, weakly developed notauli, poorly delimited frenum, propodeum with sharp median carina and plicae connected posteriorly by W-shaped carina, petiole with a basal bracing consisting of an anteriorly directed lateral and ventral flange, and the hind margin of the first gastral tergite being sinuous laterally and usually emarginate medially are the same characters defining the *Halticoptera*-group itself. So presently, *Thinodytes* can only be defined negatively. There are many South American species, some described and some not, that fit within the present definition of *Thinodytes*. Once these are investigated, it may be possible to divide *Thinodytes* into monophyletic generic units.

Halticoptera is distinguished from *Thinodytes* by a number of apomorphic character states including a bidentate clypeus, the antennal torulus located at or below the LOCL, the scape usually nonmetallic, the male maxilla with lamellately expanded palps and usually with another lobe on the stipites, and a median longitudinal carina on the petiole. *Thinodytes* has the clypeus

with variable numbers and arrangements of clypeal denticles, but no known *Thinodytes* species has a bidentate clypeus. The antennal torulus in *Thinodytes* is located distinctly above the LOCL (except in *T. petiolatus*), and the scape usually has metallic coloration. The male maxilla of *Thinodytes* lacks any expansion of the palps or any lobes on the stipites. *Thinodytes clypeatus* is the only species of *Thinodytes* that has a median carina on the petiole. *Halticoptera* species are commonly bright metallic green; those of *Thinodytes* are usually dark.

Mauleus is distinguished from *Thinodytes* by the bidentate clypeus (Fig. 13), the dorsum of the mesosoma as high as the vertex (Figs 8, 21), the median panels of the propodeum short (2× as wide as long) (Fig. 20), and the lateral flanges of the petiole enlarged and thickened (Fig. 20). In *Thinodytes*, the clypeus has various numbers and arrangements of clypeal teeth, but is never bidentate, the dorsum of the mesosoma is distinctly lower than the vertex, the median panels of the propodeum are longer (Figs. 17–19), and the basal flanges of the petiole are lamellate (Figs. 17–19).

Syntomopus is distinguished from *Thinodytes* by having an elongate pronotum (length about $\frac{1}{3}$ its width) (Fig. 22), three broad symmetrically arranged clypeal denticles (Fig. 14), and usually a flattened mesosoma (Fig. 22). The pronotum of *Thinodytes* is much shorter, those *Thinodytes* species having symmetrically arranged denticles have them fingerlike rather than broad (Fig. 11), and the mesosoma is never so flattened as it usually is in *Syntomopus* species.

Biology.—The known hosts of *Thinodytes* species are all small Diptera living in plants as leaf or stem miners.

KEY TO HOLARCTIC SPECIES OF *THINODYTES* GRAHAM

1. Petiole transverse, smooth (Fig. 17) 2
- Petiole as long as wide or longer than wide, reticulate (Figs 18–20) 4
2. Scape and legs beyond coxae pale, nonmetallic. Frenum and median panels of propodeum smooth. Plicae rounded and smoothly convergent posteriorly *santerna* n. sp.

- Scape mostly or completely metallic. Legs beyond coxae with metallic coloration or dark bands on femora and tibiae. Frenum and median panels of propodeum weakly to strongly alveolate. Plicae with distinct angle between parallel basal part and convergent posterior part 3
 - 3. Hind margin of T1 emarginate medially. Dark bands on tibiae with sharp borders (Fig. 1). Female club with apex simple *caroticus* n. sp.
 - Hind margin of T1 entire medially. Dark bands on tibiae with diffuse borders (Fig. 2). Female club with terminal spine at apex *cephalon* (Walker)
 - 4. Clypeal denticles symmetrically arranged. Petiole with weak median carina. Ovipositor exerted for length equal to that of T7 *clypeatus* (Girault)
 - Clypeal denticles asymmetrically arranged, the median denticle displaced to the left (Fig. 11). Petiole without a median carina (Figs 18–19). Ovipositor sheaths hardly exerted 5
 - 5. Costal cell with three rows of setae distally. Eye length $<4\times$ as long as the temple length (Fig. 5). Body more or less all dark *cyzicus* (Walker)
 - Costal cell with two rows of setae distally. Eye length $>4\times$ as long as the temple (Figs 3, 7). Body dark with diffuse metallic patches on head and mesosoma 6
 - 6. Male with terminal segment of funicle appearing as wide or wider than long (Fig. 4). Petiole usually less than $1.7\times$ as long as wide (Fig. 18). Female with petiole usually less than $1.5\times$ as long as wide. Both sexes with hind margins of T1 and T2 as long medially as laterally. (eastern United States and Canada) *cyzicopsis* n. sp.
 - Males with terminal segment of funicle appearing longer than wide (Fig. 6). Petiole usually more than $1.7\times$ as long as wide. Female with petiole usually more than $1.5\times$ as long as wide (Fig. 19). Both sexes with hind margins of T1 and T2 usually longer laterally than medially. (far western United States and Canada) *petiolatus* n. sp.
-

Thinodytes caroticus Heydon, **new species**
(Fig. 1)

Holotype, female.—Color: Body dark blue–green except flagellum, fore tarsus, wing veins brown; pretarsi black; knees, apical $\frac{1}{5}$ of tibiae, middle and hind tarsi white, border between the light ends and dark median band of tibiae sharp (Fig. 1).

Sculpture: Clypeus smooth; head and mesoscutum delicately and regularly alveolate; scutellum, frenum finely alveolate; median panels of propodeum obscurely alveolate.

Structure: Body length 1.2 mm. Head width $1.4\times$ height (23:17), $2.3\times$ length (23:10); anterior margin of clypeus with single broad tooth; malar distance $5\times$ length of genal concavity; eye height $1.2\times$ length (10:8); $2.0\times$ malar distance (10:5), eye length $4.0\times$ temple length (8:2); ratio of MOD, OOL, POL, LOL as 2.0:3.0:6.5:3.0; vertex rounding regularly into occiput; torulus $\frac{1}{2}$ own diameter above LOcL. Antenna with length of pedicel plus flagel-

lum $0.87\times$ head width (20:23); relative lengths of scape, pedicel, annelli, F1–6, club as 6.5:2.5:0.5:2.0:2.0:2.0:2.0:2.0:5.0; widths of F1, F6, club as 2:3:3; apical club segment simple apically, with micropilosity ventrally. Mesosoma arched dorsally, length $1.3\times$ width (25:19); dorsellum short smooth band; propodeum with basal fovea part of continuous groove across anterior margin of median panels, with short weak longitudinal carina crossing groove halfway between plica and median carina, with spiracles on anterior margin of propodeum, with nucha lunate strip and carinate anteriorly. Fore wing with ratio of lengths of submarginal, marginal, postmarginal, stigmal veins as 19.0:11.5:9.0:5.0; stigma small; basal cell bare; basal vein with row of 4 setae. Petiole conical, transverse, smooth, with median carina. Gaster fusiform, length $1.8\times$ width (30.0:16.5); hind margin of T1 emarginate medially; ovipositor sheaths hardly exerted; hypopygium extending $\frac{1}{2}$ gastral length.

Allotype, male.—Color pattern similar to holotype except basic body color dark blue; fore tarsi pale brown; pale portions of legs pale yellow-brown instead of white. Body length 1.2 mm. Antenna with length of pedicel plus flagellum $0.98\times$ head width (21.0:21.5); relative lengths of scape, pedicel, annelli, F1–6, and club as 6.0:2.5:0.5:2.0:2.0:2.0:2.0:2.0:6.0; widths of F1, F6, club as 2.5:3.0:3.0; funicular setae sparse, reclinate. Gaster ovate, length $1.5\times$ width (23:15).

Variation.—The body length of females examined varied between 1.2 and 1.8 mm and males between 1.0 and 1.4 mm. The color of the dorsum of the mesosoma varies from dark blue-green to dark blue. The dark bands on the legs are always distinct, but the intensity of their metallic coloration is variable.

Discussion.—*Thinodytes caroticus* most closely resembles *T. cephalon* because both species are dark in color; have a single, broad, asymmetrically placed clypeal denticle; and have smooth, transverse petioles. *Thinodytes caroticus* differs from *T. cephalon* in the following: 1. The hind margin of T1 is emarginate in *T. caroticus*, but straight in *T. cephalon*. 2. The basal vein of the fore wing is setose in *T. caroticus*, but bare in *T. cephalon*. 3. The median panels of the propodeum are weakly sculptured in *T. caroticus*, but distinctly alveolate in *T. cephalon*. 4. The hypopygium extends about $\frac{1}{2}$ the length of the gaster in *T. caroticus*, but about $\frac{2}{3}$ the gastral length in *T. cephalon*. 5. The dark bands on the tibiae are distinct with sharp borders in *T. caroticus*, but are less distinct and have diffuse borders in *T. cephalon*. These distinctive tibial color bands are unique to *T. caroticus* and will identify the species at a glance (Fig. 1).

Etymology.—The species name comes from the Greek *karotikos*, meaning stupefying or soporific, and refers to the general nondescript appearance of this species.

Type Material.—The holotype, allotype (both UCDC) and one male paratype were

all reared by the author from the leaf mines of *Calycomyza promissa* (Frick) (Diptera: Agromyzidae) collected 30 June 1985 on the South Farms of the University of Illinois, near Champaign, Illinois. Fifty-nine additional paratypes seen were collected as follows (CNCI, INHS, SEMC, UCDC, USNM): Bermuda. DEVONSHIRE PARISH: Devonshire Marsh, 27.VI.1988, 1 male. PAGOT PARISH: Berry Hill Road, 29.VI.1988, 2 females, 3 males; Botanical Garden, 27.VI.1988, 1 female; Camdon Marsh, 29.VI.1988, 1 female. SMITHS PARISH: Spittal Pond, 27.VI.1988, 1 female. Canada. ONTARIO: Chatham, 1952 (mass reared from Hessian fly straw), 1 male. United States. CALIFORNIA: Hawthorne, IX.1940 (ex Aster blotch), 3 females, 1 male; Jepson Prairie Preserve (13 km s. Dixon), 20.V.1983, 1 female; Lake Hennessy (11 km ese. St. Helena), 28.X.1990, 1 female; Los Angeles County (bred from dipterous leaf miner), 1 female; Sacramento, 16.IX.1924 [ex *Agromyza pusilla* (prob.=*Liriomyza pusilla*)], 1 female; Soquel, 26.VIII.1948 (ex *Agromyza* sp.), 2 females, 1 male; 11 km e. St. Helena (Lake Hennessey), 28.X.1990 (on *Baccharis*), 1 female, 7.IX.1991 (on *Heracleum*), 1 male; 6 km e. Suisun City, 11.VIII.1990, 2 males; 1000 Palms, 29.III.1977, 1 female; Westwood Hills (Los Angeles County), 5.XI.1940 (ex serpentine leaf miner in Zinnia), 4 females, 1 male. FLORIDA: Bradenton, 27.XI.1946 [ex *Liriomyza pissilla* (prob.=*Liriomyza pusilla*)], 1 male; Jacksonville, 2 females. GEORGIA: Savannah, 5.VI.1943 (parasite of goldenrod leafminer), 3 females. ILLINOIS: South Farms of the University of Illinois, 19.V.1985, 1 female; White Heath, 24.IX.1939, 1 female. INDIANA: 4 miles s. New Harmony (Harmony State Park), 28.VI.1983, 2 females; 2 miles s. New Lisbon, 14.VII.1981, 1 male. IOWA: Sioux City (reared from leaf miner on sunflower leaf), 1 female, 5.VIII.1921 (reared from mine of leaf on sunflower), 1 female. KANSAS: Lawrence, 14.V.1955, 1 female. MINNESOTA: Albert Lea,

26.VII.1960, 1 female. NEW MEXICO: Cimarron, 1909, 1 female; Springer, 1909, 1 female, 3 males. TEXAS: Clarendon, 19.IX.1905 (on *Grindelia squarrosa* (Pursk) Dunal (Compositae), 1 female; Ennis, 27.IX.1905 [ex dipterous leaf miner of *Machaeranthera annua* (Rydb.) Shinner (Compositae)], 2 females; Roma, 26.III.1948 (ex pupa of dipterous leaf miner), 3 females, 3 males.

Biology.—This species has been reared from leaf-mining Agromyzidae, mostly on Compositae. Known hosts include *Calycomyza promissa* (Frick) and *Liriomyza pusilla* (Meigen). Because *L. pusilla* is a Palearctic agromyzid species (Spencer 1976) and is not known from the Nearctic region (Spencer and Steyskal 1986), it is likely that this host record is in error. There is one record from Chatham, Ontario from Hessian fly straw. *Thinodytes caroticus* was also reared from leaf miners on *Machaeranthera annua*, Zinnia, goldenrod, sunflower, and "Aster". It has been reared from both linear-mining and blotch-making leaf miners. Other plant associations of a more uncertain nature include the composites *Baccharis* sp., *Heracleum* sp., and *Grindelia squarrosa*.

Thinodytes clypeatus (Girault)

Polycystus clypeatus Girault, 1918:128. Holotype, female (USNM); Hym. Type No. 20682; (examined).

Thinodytes clypeatus (Girault): Heydon, 1989: 193.

Redescription.—Holotype, female. Color: Mesosoma, petiole black, with blue tints on propodeum and pleural regions; gaster dark brown; legs with basal $\frac{2}{3}$ of femora brown, remainder of legs white.

Sculpture: Dorsum of mesosoma regularly and delicately reticulate; median panels of propodeum weakly alveolate; petiole alveolate.

Structure: Head with anterior margin of clypeus with three symmetrically arranged fingerlike denticles, torulus above LOCL. Antenna with lengths and widths

of segments as follows (in μm): scape 19.5 \times 3.6; pedicel 6.0 \times 4.5; annelli 2.6 \times 3.6: F1 5 \times 6: F2 4.6 \times 6.0: F3 5.2 \times 6.2: F4 4.6 \times 6.5: F5 4.6 \times 6.8: F6 missing; club 13.4 \times 6.8; club simple apically. Mesosoma with dorsum rather flat, length 1.4 \times width (33:24); pronotum with collar width 11 \times length (22: 2), sides converging posteriorly; notauli shallow posteriorly; scutellum with two pairs of lateral setae, frenum almost indistinguishable from remainder of scutellum; propodeum with length of median panels 0.45 \times width, with row of foveae separated by carinae along anterior margin, spiracle on anterior margin of propodeum, nucha a raised smooth crescent. Fore wing with relative lengths of submarginal, marginal, postmarginal, stigmal veins as 21:12:11:6; stigma large, height $\frac{1}{2}$ distance between stigma and anterior margin of wing; basal cell with one seta; basal vein with three setae. Petiole length 1.2 \times width (6:5); with weak median carina; lacking lateral setae. Gaster fusiform, length 1.7 \times width (31.0: 18.5); T1 emarginate medially; hypopygium extending $\frac{2}{3}$ length of gaster; ovipositor sheaths exerted for length equal to that of T7.

Discussion.—The holotype has the head removed and crushed on a slide. *Thinodytes clypeatus* differs from all other described *Thinodytes* species because it has an enlarged stigma, exerted ovipositor sheaths, and a median carina on the petiole. *Thinodytes clypeatus* has three symmetrically arranged denticles like *Syntomopus* species, but *T. clypeatus* differs from *Syntomopus* species in several ways. The denticles of *T. clypeatus* are fingerlike lobes like those of the other *Thinodytes* species with three denticles, whereas the denticles of *Syntomopus* species are rather broadly triangular (Fig. 14). The pronotal collar of *Thinodytes clypeatus* is short, eleven times as wide as long; the pronotal collar in *Syntomopus* is only about three times as wide as long (Fig. 22). Most species of *Halticoptera* have a median carina on the petiole, but there are no other characters to indi-

cate a particularly close relationship between *T. clypeatus* and *Halticoptera*.

Distribution and Biology.—The type specimen was reared from a leaf miner on corn on 2 May 1916, on St. Vincent, British West Indies by F. Watts. De Santis (1979) reports this species from Barbados also, and gives the name of its host as *Agromyza parvicornis* Loew (Diptera: Agromyzidae).

Thinodytes cephalon (Walker),

new combination

Figs 1, 17

?*Pteromalus Rhæo* Walker, Walker 1839b:88–89.

Lectotype, female (BMNH); Hym. Type No. 5.772 (examined).

Gastrancistrus cephalon Walker 1843:30. Lectotype, male (BMNH); Hym. Type No. 5.661 (examined).

Bubekia fallax Gahan, 1933:114–116. Holotype, female (USNM); Type No. 44841 (examined). Allen and Painter, 1937:225. Nikol'skaya, 1937:25. Peck, 1951:538. Thompson, 1958:587. Peck, 1963:610–611. Morrill and Kieckhefer, 1971:1130. Allen and Pienkowski, 1973:616, 617. Burks, 1979:789. Hendrickson, 1979:300, 302. n. syn.

Discussion.—*Thinodytes cephalon* is easily distinguished by its single broad clypeal denticle, apical spine on the female club, notauli traceable to the hind margin of the mesoscutum as impressed lines, bare dorsal vein, smooth and short petiole (Fig. 17), and first gastral tergite having the hind margin entire.

A possible senior synonym of *T. cephalon* is *Pteromalus rhæo* described from Chiloe Island, Chile. The lectotype female (designated herein) of *P. rhæo* is unfortunately missing the head. It appears similar to specimens of *T. cephalon* examined, of which many specimens in my collection and the CNC collection were from Chiloe Island, but it is significantly larger than any other specimen examined. The median panels of the propodeum in *P. rhæo* are entirely rugose and the plicae are posteriorly divergent. In other *T. cephalon* examined, the median panels have few ru-

gae which are located mostly posteriorly, and the plicae are parallel. The hind tibia in *P. rhæo* is almost uniform in color; in *T. cephalon*, the hind tibia are distinctly dark over the middle half or more. *Pteromalus rhæo* may be within the range of variation of what is recognized as *T. cephalon*, but I am reluctant to formally synonymize the name until more is known about the range of variation of *T. cephalon* in South America.

Distribution.—*Thinodytes cephalon* is one of the most commonly collected New World pteromalids. Its distribution extends throughout most of North and South America (from Chile to Canada and also Bermuda).

Biology.—*Thinodytes cephalon* is a parasitoid of dipterous larvae that mine leaves or grass stems. *Thinodytes cephalon* was originally described from puparia of the Hessian fly, *Phytophaga destructor* (Say) (Diptera: Cecidomyiidae) (Gahan 1933). It has also been reared from the wheat stem maggot, *Meromyza americana* Fitch (Diptera: Chloropidae), in a number of studies (Gahan 1933; Allen and Painter 1937; and Morrill and Kieckhefer 1971). Allan and Painter report that *T. cephalon* probably oviposits into the larval stage of this host. One additional host added herein is *Liriomyza trifoliarum* Spencer (Diptera: Agromyzidae) on alfalfa.

Thinodytes cyzicopsis Heydon,

new species

Figs. 3, 4, 18

Holotype, female.—Color: Head, mesosoma black with metallic green patches as follows: entire dorsellum, pairs of spots alongside median ocellus, lateral hind corners of pronotum and upper epimeron; metallic blue patches as follows: on inner orbits, anterior part of lateral lobe of scutum and propodeum. Antenna with scape, pedicel dark blue; flagellum black. Petiole black. Gaster brownish black with metallic blue reflections dorsally, green ventrally. Legs with coxae black with weak blue re-

flections; trochanters, femora brownish black with weak green reflections, knees yellow, tibiae with diffuse-edged dark brown band extending $\frac{2}{3}$ their length; fore tarsi brown; middle and hind tarsi with pretarsi black, remainder yellow.

Sculpture: Head, mesosoma, regularly and delicately alveolate; frenum, propodeum shallowly and indistinctly alveolate; petiole finely alveolate.

Structure: Body length 1.6 mm. Head width $1.2 \times$ height (27:22), $2.2 \times$ length (27:12); anterior margin of clypeus with three minute asymmetrically arranged apical denticles; genal concavity absent; eye height $1.4 \times$ length (13:9), $1.9 \times$ malar distance (13:7), length $4.5 \times$ temple length (9:2) (Fig. 3); ratio of MOD, OOL, POL, LOL as 2.5:4.0:7.0:3.0; vertex rounding smoothly into occiput; torulus $\frac{1}{2}$ own diameter above LOcL. Antenna with length of pedicel plus flagellum $1.0 \times$ head width (27:27); relative lengths of scape, pedicel, annelli, F1–6, club as 11.0:3.0:1.0:2.5:3.0:2.75:2.75:2.5:2.5:7.0; widths of F1, F6, club as 3.0:3.5:3.5, F1–4 appearing quadrate, F5–6 slightly transverse; club simple apically, with minute patch of micropilosity on terminal segment. Mesosoma arched dorsally, length $1.6 \times$ width (36:22); pronotum with humeral angles squared; mesoscutum with notauli shallow; dorsellum bandlike, short, weakly alveolate; propodeum with basal fovea bordered mesally by sinuous carina; nucha a raised band, weakly carinate anteriorly; spiracle $< 0.5 \times$ own diameter from anterior margin of propodeum. Fore wing with ratio of lengths of submarginal, marginal, postmarginal, stigmal veins as 25:13:14:8; stigma small, maximum width only slightly more than stigmal vein width; basal cell bare; basal vein setose. Petiole length $1.2 \times$ width (6:5); without median carina; with one pair of lateral setae. Gaster length $1.4 \times$ width (31:22); hypopygium extending to about $\frac{2}{3}$ length of gaster; ovipositor sheaths hardly exerted.

Allotype, male.—Color similar to holo-

type except frons blue, mesoscutum with a pair of large diffuse green spots; axilla green. Body length 1.3 mm. Antenna (Fig. 4) with length of pedicel plus flagellum $1.0 \times$ head width (24:23); relative lengths of scape, pedicel, annelli, F1–6, club as 7.0:3.0:1.0:2.0:2.5:2.5:2.5:2.5:2:6.5; widths of F1, F6, club as 2.0:2.5:2.5; setae fine, reclinate. Petiole length $1.2 \times$ width (5:4) (Fig. 18). Gaster ovate, length $1.2 \times$ width (20.0:16.5).

Variation.—The body color varies from mostly dark, like the holotype, to the pattern shown by the allotype male. The intensity, size, number, and hue of the metallic spots on the body are highly variable. The color of the metallic patches varies from coppery green to green to blue-green. The body length ranges between 1.4 and 1.8 mm in females and 1.2 and 1.7 mm in males. The length of the marginal vein varies from 0.9 to 1.2 times the length of the postmarginal vein but averages about equal its length [$x = 1.02 \pm (S.E.) 0.02$ ($n = 12$)]. The petiole averages 1.39 ± 0.045 ($n = 7$, range 1.2–1.5) times as long as wide in the females and 1.57 ± 0.061 ($n = 7$, range 1.2–1.9) times in males (Fig. 18). The pair of lateral setae on the petiole are sometimes difficult to see because they tend to lie near the anterior flanges of the petiole.

Discussion.—*Thinodytes cyzicopsis* resembles the Palearctic species *T. cyzicus* (Thomson), but differs from that species in the following: 1. *Thinodytes cyzicopsis* has a series of metallic patches on the body, which are lacking in *T. cyzicus*. 2. The ratio of the eye length to temple length averages 4.25 ± 0.12 ($n = 6$, range 3.8–4.5) in female *T. cyzicopsis* (Fig. 3) but measured only 2.3 and 3.6 in two female *T. cyzicus* specimens examined (Fig. 5). 3. The costal cell of the fore wing of *T. cyzicopsis* has two rows of setae distally, whereas there are three rows distally in the costal cell of *T. cyzicus*. 4. The petiole has a pair of lateral setae in *T. cyzicopsis*, which are lacking from *T. cyzicus*.

Thinodytes cyzicopsis and *T. petiolatus* are very similar species and specimens cannot always be confidently separated. These two species are distinct from other *Thinodytes* in their common possession of a similar pattern of metallic patches on the head and mesosoma. Individuals of *T. cyzicopsis* differ from those of *T. petiolatus* in the following: 1. The ratio of eye height to malar distance in *T. cyzicopsis* averages 1.74 ± 0.035 ($n=8$, range 1.5–1.8) in females and 2.04 ± 0.032 ($n=9$, range 1.9 to 2.0) in males; in *T. petiolatus* the ratio is 1.48 ± 0.23 ($n=10$, range 1.4 to 1.6) in females and 1.77 ± 0.038 ($n=10$, range 1.6 to 2.0) in males. 2. All funicular segments of the male antenna are transverse to quadrate in *T. cyzicopsis*; all funicular segments are usually longer than wide in male *T. petiolatus*. 3. The ratio of petiole length to width in *T. cyzicopsis* averages 1.39 ± 0.045 ($n=7$, range 1.2 to 1.5) in females and 1.57 ± 0.061 ($n=7$, range 1.2 to 1.9) in males; in *T. petiolatus* it averages 1.93 ± 0.062 ($n=10$, range 1.5 to 2.0) in females (Fig. 19) and 1.95 ± 0.071 ($n=10$, range 1.6 to 2.4) in males. 4. The first gastral tergite in *T. cyzicopsis* is about as long medially as laterally, whereas T1 is often shorter medially than laterally in *T. petiolatus*. 5. The hind margin of T2 is straight to just noticeably concave in *T. cyzicopsis*, whereas it is usually distinctly concave in *T. petiolatus*. 6. The terminal segment of the male funicle appears quadrate to slightly transverse in *T. cyzicopsis*, whereas it appears elongate in *T. petiolatus*. In addition to these structural characters, *T. cyzicopsis* is found east of the Rocky Mountains, and *T. petiolatus* occurs from the Rockies west.

Type Material.—The holotype (CNCI) is from Kouchibouquac National Park, New Brunswick, and was collected 9 August 1977 by S. J. Miller. The allotype (USNM) is from Ithaca, New York, and was collected on vernal alfalfa on 22 June 1968 by A. G. Wheeler. Sixteen paratypes were collected as follows (CNCI, UCDC, USNM):

Canada. ALBERTA: Elkwater Lake, 21.VII.1956, 1 female; Lethbridge, 1 female. NEW BRUNSWICK: Kouchibouquac National Park, 20.IX.1977, 1 female. NOVA SCOTIA: Alton, IX.1964 [ex *Phytobia* (*Calycomyza*) *solidaginis* on *Solidago*], 1 male; Crosby, 31.VII.1952 (on apple), 1 male. ONTARIO: Ottawa, 22.VI.1972 (swept from *Salix blanda*), 1 male, 29.VI.1972 (swept from *Salix blanda*), 3 males, 24.VII.1972 (swept from *Salix blanda*), 1 male. QUEBEC: Lac Brule, 21.VII.1947, 1 female, 25.VII.1947 (swept from *Rosa rugosa*), 1 female, 9.VIII.1945, 1 female. United States. ILLINOIS: 2 miles e. Shumway, 7.VII.1980, 1 female; South Farms of the University of Illinois, nr. Champaign, 23.VI.1981, 1 male. MASSACHUSETTS: Hopkinton, 9.VIII.1951 (ex *Ilex* leaf miner), 1 female. NEW MEXICO: Mesilla, 4.V.1909, 1 female. WEST VIRGINIA: Winchester, 16.VI.1964, 1 male, 17.VI.1964, 1 male.

Etymology.—The species name is derived from the species name of *Thinodytes cyzicus* and the Greek suffix *-opsis*, meaning like or similar in appearance, and refers to the morphological similarity between *T. cyzicopsis* and *T. cyzicus*.

Biology.—Known hosts of *T. cyzicopsis* include *Phytobia* (*Calycomyza*) *solidaginis* (Agromyzidae)[on *Solidago* sp. (Compositae)] and an *Ilex* leafminer. The species has also been taken on *Salix blanda* (Salicaceae), *Rosa rugosa* (Rosaceae), and alfalfa. *Salix* and *Rosa* are probably primarily nectar sources because neither has many leaf-mining agromyzids, but these plants are important sources of nectar and/or honeydew for many parasitic Hymenoptera.

Thinodytes cyzicus (Walker)

Miscogaster cyzicus Walker, 1839a:200. Lectotype, female (BMNH); Hym. Type No. 5.2570 (examined).

Syntomopus cyzicus (Walker): Walker, 1846:28. Schmiedeknecht, 1909:376.

Dicyclus circulus Thomson, 1876:253. Lectotype, female (LUND), not seen.

Thinodytes cyzicus (Walker): Graham, 1956:261. Graham, 1969:167. Askew, 1970:380. Hedqvist, 1975:180. Bouček, 1977:56. Kamijo, 1978:457. Takada and Kamijo, 1979:21, 22, 23, 25. Hedqvist, 1983:167. Bouček and Rasplus, 1991:32.

Thinodytes petiolatus Heydon,
new species
Figs 6, 7, 11, 19

Holotype, female.—Color: Body black but frenum, metanotum coppery; frons, vertex, gena, lateral region of pronotum, lateral lobe of mesoscutum, middle lobe of mesoscutum with pair of large diffuse metallic patches, anterior lateral corner of axilla dark metallic green; gaster with greenish reflections. Antenna with scape dark green; remainder brown, pedicel with weak green reflections. Legs with coxae black with greenish reflections; femora brown with greenish reflections; remainder of legs mostly yellow-brown, tibiae with broad diffuse brown band mesally, apical two tarsi brown. Wing veins pale reddish brown.

Sculpture: Clypeus weakly alveolate; face alveolate, cells elongate in radiating fashion from clypeus; remainder of head alveolate; mesoscutum, scutellum delicately and regularly alveolate except frenum smooth; median panels of propodeum alveolate; petiole finely alveolate.

Structure: Body length 1.8 mm. Head width $1.4\times$ height (28:21), $2.6\times$ length (28.5:11.0); clypeus with three small asymmetrically arranged clypeal denticles (Fig. 11); weak genal concavity extending $\frac{1}{2}$ malar distance; eye height $1.3\times$ length (12.0:9.5), $1.5\times$ malar distance (12:8), length $4.8\times$ temple length (9.5:2.0) (Fig. 7); ratio of MOD, OOL, POL, LOL as 2:4:7:3; vertex rounding regularly into occiput; antennal torulus just above LOcL. Antenna with length of pedicel plus flagellum $0.91\times$ head width (26:28.5); ratio of lengths of scape, pedicel, annelli, F1–6, club as 11.5:3.5:1.0:2.5:2.5:2.5:2.5:2.5:6.0; widths of F1, F6, club as 2:3:3; club simple apically, with small patch of micropilosity ventrally on apical segment. Mesosoma arched dorsally, length $1.7\times$ width (37:22); notauli shallow posteriorly; propodeum (Fig. 19) with basal fovea margined mesally by long sinuous carina; nucha a weakly

Discussion.—The synonymy of *Dicyclus circulus* with *Thinodytes cyzicus* is accepted on the authority of Graham (1969). *Thinodytes cyzicus* resembles *T. cyzicopsis* and *T. petiolatus*, because all three species have three small, sharp, asymmetrically arranged clypeal denticles (Fig. 11) and a long, reticulate petiole. Besides the geographic separation of their ranges, *T. cyzicus* can be distinguished from the two Nearctic species by its body color. *Thinodytes cyzicus* is uniformly dark and lacks the distinctive diffuse metallic patches on the head and mesosoma present in *T. cyzicopsis* and *T. petiolatus*. *Thinodytes cyzicus* also has three rows of setae distally in the costal cell, whereas *T. cyzicopsis* and *T. petiolatus* have only two rows. The eye length in *T. cyzicus* is $4\times$ or less the length of the temple (Fig. 5), whereas *T. cyzicopsis* and *T. petiolatus* have the eye length more than $4\times$ the length of the temple (Figs 3, 7).

Distribution.—*Thinodytes cyzicus* occurs throughout the Palearctic region, from Britain to Japan (Graham 1969; Bouček 1970; Kamijo 1978).

Biology.—The hosts of *T. cyzicus* are all Agromyzidae. Askew (1970) recorded this species from an agromyzid, probably *Phytomyza atricornis* Meigen, on *Senecio jacobaea* Linnaeus. Kamijo (1978) recorded *T. cyzicus* from *Chromatomyia horticola* (Goureau) (Diptera: Agromyzidae) on pea and from an agromyzid on *Lathyrus maritimus*. Takada and Kamijo (1979) recorded *T. cyzicus* as emerging from the puparium of *Chromatomyia horticola* and speculated that *T. cyzicus* may parasitize the larval stage of its host.

sculptured band, carinate anteriorly; spiracle $<0.5\times$ own diameter from anterior margin of propodeum. Fore wing with relative lengths of submarginal, marginal, postmarginal, stigmal veins as 27.0:14.5:15.0:9.0; stigma small; basal vein with row of setae along length. Petiole (Fig. 19) length $2.0\times$ width (8:4); without median carina; with two pairs of lateral setae. Gaster ovate-acuminate, length $1.4\times$ width (33:24); hind margin of T1 strongly sinuous laterally, emarginate mesally; ovipositor sheaths hardly exerted; hypopygium extending $\frac{2}{3}$ gastral length.

Allotype, male.—Body color similar to holotype except metallic spots more diffuse and extensive; frenum, metanotum blue-green; dark bands on tibiae very weak. Body length 1.3 mm. Antenna (Fig. 6) with length of pedicel plus flagellum $1.1\times$ head width (28:25); ratio of lengths of scape, pedicel, annelli, F1–6, club as 9.0:3.5:1.0:2.5:3.0:3.0:3.0:3.0:8.0; widths of F1, F6, club as 2:2:3; setae of flagellomeres fine, reclinate. Petiole length $2.0\times$ width (8:4). Gaster length $1.2\times$ width (20:16); truncate apically.

Variation.—The body color varies from like that of the holotype to very dark, with the green areas on the head and the mesosoma reduced and obscure, the frenum and metanotum green, and the tibiae dark metallic green. The body length of females examined varied between 1.3 and 1.8 mm and males varied between 1.0 and 1.6 mm. The sinuous carina on the propodeum sometimes extends only $\frac{1}{4}$ the length of the propodeum. The row of setae on the basal vein sometimes curls proximally, running a short distance along the cubital vein.

Discussion.—*Thinodytes petiolatus* and *T. cyzicopsis* are very similar species and are distinct from other *Thinodytes* species in the similar pattern of metallic patches on an otherwise dark body. Individuals of *T. petiolatus* and *T. cyzicopsis*, especially females, cannot always be distinguished with absolute certainty. Characters to sep-

arate these two species are given in the discussion section for *T. cyzicopsis*. The hind margin of T2 in many specimens of *T. petiolatus* is distinctly concave, but the visibility of this character depends on how the specimen has dried. This character is more distinct in the males than in the females.

Type Material.—The holotype (USNM) was collected at Roseworth, Idaho, on 19 June 1931, on *Salsola pestifer* by D. E. Fox and the allotype (USNM) was collected at Twin Falls, Idaho, on 5 August 1920 by R. H. Smith. Sixty paratypes were collected as follows (CNCI, INHS, UCDC, USNM): Canada. ALBERTA: Banff (Sunshine Lodge, 7500'), 24.VII.1962, 1 female; Elkwater, 9.VI.1956, 1 male; Elkwater Lake, 21.VII.1956, 1 male; Lethbridge, 7.VI.1956 (swept from barley), 1 female, 5.VIII.1956 (swept from barley), 1 male; nr. Lethbridge, 1924.1925, 1 female. BRITISH COLUMBIA: Bowser, 28.V.1955, 1 female; McQueen Lake, 10 miles n. Kamloops, 18.VI.1973, 1 male. United States. ARIZONA: Mesa, 3.VI.1958 (swept from alfalfa), 1 male. CALIFORNIA: Albany, 29.IV.1958, 1 male; Alpine Lake, VI.1971, 1 female; Apple Valley, 8.V.1955, 2 males; 15 miles w. Baker, 6.V.1977, 2 females, 1 male; Boca, 22.VII.1970, 1 female; Bolinas, 5.X.1975, 2 males; Camino, 21.VII.1948 (ex *Phytomyza aquilegiana*), 10 females; Cerro Noroeste (sw. corner of Kern Co.), 15.VII.1965, 1 female; Cuyler Harbor (San Miguel Island), 11.VII.1970, 1 male; Darwin Falls (nr. Panamint Springs), 29.III.1984 (on *Encelia*), 1 male; Emeryville, 28.V.1958, 1 male; Eureka Dunes (Inyo Co.), 15.V.1979, 1 male; Lake Tenaya, 23.VII.1949 (host *Recurraria milleri*), 1 female; Lake Tahoe, 29.VI.1927, 1 female; Lily Pond (alpine lake), VI.1971, 1 female; Los Angeles (*Agromyza playptera* Thom.), 1 female; Los Angeles Co., 1 male; McClure Beach (Marin Co.), 18.VII.1970, 1 male; Mt. Ingalls (Placer Co.), 11.VII.1964, 1 male; near Nicasio, 15.II.1991 (sweeping *Salix*), 2 males; 22 miles w. Panamint Springs,

7.V.1961, 2 males; Placer Co., VIII, 1 male; Sagehen Creek (near Hobart Mills), 24.VI.1970, 1 female, 21–25.VI.1982 (sweeping *Prunus*), 1 male, 12.VII.1972, 1 male, 11–15.VII.1982, 1 female, 23.VII.1968, 1 female, 1.VIII.1970, 1 female; San Bernardino Co., San Gorgonio Wilderness, 19.VII.1982, 1 male; Santa Cruz, 22.VIII.1948 (ex *Phytomyza* sp. B), 1 female; Santa Rosa, 25.V.1990, 2 males; Sheppard Pass Trail (Inyo Co.), 16.VII.1985 (on *Sphenosciadium capitellatum*), 1 male; Shively, 19.VI.1959, 1 female; Sonora Pass (Mono Co., 9624'), 20.VIII.1960, 1 female; Soquel, 26.VIII.1960 (ex *Agromyza* sp.), 2 females; Titus Canyon (Death Valley National Monument), 24.III.1984 (on *Cownia mexicana*), 1 male; Tomales Bay State Park (Marin Co.), 14.IV.1961, 1 male; Trinidad, 24.IX.1977, 1 female; Truckee, 20.VII.1970, 1 female; White Water, Snow Creek (1500'), 29.III.1955, 1 male; 6 miles w. Bassett's (Yuba Pass), 9.VII.1970, 2 females, 2 males. COLORADO: Chambers Lake (Larimer Co.), 16.VIII.1966, 1 male; 16 km n. Colorado Springs, 25.VII.1991, 1 male; Ft. Collins, 20.VIII.1895 (on boxelder foliage), 1 female, 1 male; Glacier Basin, Rocky Mountain National Park, 24.VII.1977, 1 male; Echo Lake (Mt. Evans, 10,500'), 4.VIII.1961, 1 female. IDAHO: Boise, 28.V.1984 (Malaise trap), 2 males; Buhl, 27.V.1929 (1 & 5¹), 2 males; Burley, 14.VI.1930 (3), 1 female, 9.VII.1931, 1 female; Eden, 11.VIII.1930 (2), 1 female; Hobbs Butte, 22.V.1931, 1 male, 6.VI.1931, 1 male; Hollister, 16.V.1931 (3), 1 male, 20.V.1931, 2 males, 2.VI.1931, 1 female, 1 male, 5.VI.1931 (3), 1 female, 7.VI.1931 (3 & 5), 1 female, 13.VI.1931, 1 female; Hubbs Butte, 22.V.1931, 1 male, 6.VI.1931, 1 male; Jerome, 11.VIII.1930 (2), 1 male; Kimberly, 27.VI.1931, 2 females; Milner, 29.V.1930

(5), 1 male; Moscow, 6.VIII.1926, 1 male; Murtaugh, 29.V.1930 (3 & 5), 1 male; Oakley, 7.VIII.1929 (1, 3 & 5), 1 female; Rupert, 29.V.1930, 1 female; Tuttle, 22.V.1931 (4), 1 female; Twin Falls, 7.VI.1930, 1 male; Wendell, 22.V.1931 (5), 3 males. MONTANA: Big Butte, 8.VIII.195?, 1 male. OREGON: Corvallis, 15.VI.1981, 1 male, 26.VI.1985, 1 female, 3 males; Near Corvallis (St. Mary's Peak), 15.VIII.1984 (roadside vegetation), 1 female; Eugene, 6–12.VI.1984 (Malaise trap), 1 female, 11 males; McKinzie Pass (Mt. Washington Wilderness), 17.VIII.1984, 2 females, 20.VIII.1984, 5 females, 2 males; 1 mile w. McKinzie Pass, 1 female, 1 male. UTAH: Logan Canyon, 21.VII.1976, 1 female; Monte Cristo, 6.VII.1976, 1 male; Myton, 3 males; Wellsville, 13.V.1964, 1 male; 1.5 miles w. Wild Horse Butte (Wild Horse Creek), 31.VII.1982, 1 female. WASHINGTON: San Juan Island (Barney's Place), 23.VII.1944, 1 male. Vancouver, 15.VI.1911, 1 female, 1 male, 16.VI.1911, 1 male, 20.VI.1911, 1 female. WYOMING: Kemmerer, 12.VII.1985 (*Eriogonum*), 2 females, 13.VII.1985 [*Artemesia spinosa* (?=*spinescens* D.C. Eaton)], 1 male; Snowy Range, 23.VIII.1951, 2 females, 1 male.

Etymology.—The species name refers to the long petiole, characteristic of this species.

Biology.—The host(s) of *T. petiolatus* is unknown but it has been taken in association with a number of plants, such as *Artemesia* sp., *Descurainia sophia*, *Eriogonum*, *Salsola pestifer*, and *Sisymbrium altissimum* in Idaho and *Encelia* in California. It has also been collected in association with crop plants, such as beets in Idaho and barley in Alberta.

Thinodytes santerna Heydon, new species

Holotype, female.—Color: Body black with blue–green reflections on vertex, side lobes of mesoscutum, scutellum, gaster; coppery reflections on frenum and dorsellum; yellow–green reflections on middle lobe of scutellum and propodeum. Anten-

¹ The host plants for the specimens from Idaho are numbered as follows: 1= *A. rosae*. 2= *Beta vulgaris* L. 3= *Sophia sophia* (= *Descurainia sophia* (L.) P.B. Webb). 4= *Salsola pestifer* A. Nelson. 5= *N. (orta) altissimum* or *S. altissima* (= *Sisymbrium altissimum* L.).

na with scape yellow, flagellum brown dorsally, brownish white ventrally. Legs yellow beyond coxae, tarsi white, pretarsi brown. Fore wing veins pale brown.

Sculpture: Clypeus alveolate; frenum, dorsellum, propodeum smooth; gaster with T5–7 coriaceous, remainder smooth.

Structure: Body length 1.6 mm. Head width $1.4\times$ height (28:20), $2.3\times$ length (28:12); clypeus with three small symmetrically arranged clypeal denticles; weak genal concavity extending $\frac{1}{3}$ malar distance; eye height $1.3\times$ length (11:10), $2.2\times$ malar distance (11:6), length $5.0\times$ temple length (10:2); ratio of MOD, OOL, POL, LOL as 2:3:6:3; vertex rounding regularly into occiput; antennal torulus just above LOCL. Antenna with length of pedicel plus flagellum $0.86\times$ head width (24:28); ratio of lengths of scape, pedicel, annelli, F1–6, club as 10:3:1:2:2:2:2:2:6; widths of F1, F6, club as 2:2:2; club simple apically, with small patch of micropilosity ventrally on apical segment. Mesosoma arched dorsally, length $1.5\times$ width (32:22); notauli shallow posteriorly; propodeum with basal fovea obscure, nucha lunate strip and carinate anteriorly, spiracles on anterior margin of propodeum. Fore wing with relative lengths of submarginal, marginal, postmarginal, stigmal veins as 24:12:12:6; stigma small; basal vein with row of setae along length. Petiole transverse, smooth. Gaster ovate acuminate, length $1.6\times$ width (36:23); hind margin of T1 nearly straight, slightly convex mesally; hypopygium extending $\frac{1}{2}$ gastral length.

Discussion.—This species is distinct from all other *Thinodytes* species by the characters listed in the key: scape and legs beyond coxae pale, nonmetallic; frenum and median panels of propodeum smooth; plicae rounded and smoothly convergent posteriorly. In these characters, *T. santerna* is phenetically similar to species of *Noto-glyptus*.

Type Material.—The holotype (USNM) was collected 3 April 1984, at the Eagle Borax Works in Death Valley National

Monument, Inyo County, California (USA) by E. E. Grissell on *Distichlis* in a brackish marsh.

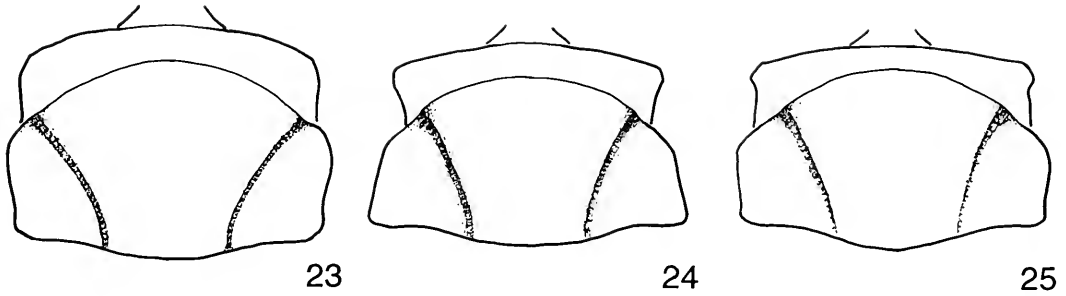
Etymology.—The specific epithet of this species is from the Latin noun *santerna*, meaning borax, and refers to the locality where the type specimen was collected.

Biology.—Nothing is known of the host(s) of *T. santerna*.

Mauleus Graham, 1981

Type Species: *Mauleus maderensis* Graham, 1981 (examined); original designation.

Description.—Body very dark green or blue; scape brownish yellow, nonmetallic. Head, pronotum, mesoscutum, scutellum (including frenum), dorsellum, median panels of propodeum, petiole alveolate; gastral tergites nearly smooth. Head with clypeus bidentate (left tooth compound) (Fig. 13), lateral part of mouth margin with short shallow genal concavity; antennal torulus $1\times$ own diameter above LOCL. Antenna with scape cylindrical, $\geq 6\times$ as long as wide; flagellum length less than head width in females, about equal to head width in males; funicular segments cylindrical; MPP sensilla in single row; female club simple apically and with small patch of micropilosity on apical segment. Male maxilla with palps slender, stipites unenlarged. Mesosoma (Figs 8, 21) arched dorsally; pronotum with collar short (Figs 23–25), nearly level with vertex dorsally, anterior edge rounded; mesoscutum with notauli shallow, impressed lines at most; scutellum as long as wide, lacking anterior median groove, frenum indistinguishable from remainder of scutellum; dorsellum short, length about equal to length of ridge across anterior margin of propodeum; propodeum (Fig. 20) with median panels short (width about $2\times$ median length), plicae and median carina well developed and connected posteriorly by W-shaped carina; spiracles strongly ovate almost linear. Fore wing with relative lengths of veins as follows: submarginal >



Figs. 23–25. 23, *Mauleus maderensis* Graham, female pronotum and mesonotum; 24, *Mauleus iligneus* n. sp., female pronotum and mesonotum; 25, *Mauleus venetus* n. sp., female pronotum and mesonotum.

marginal > postmarginal > stigmal; stigma small, width about 2X width of stigmal vein; costal cell with complete row of setae and sometimes a partial second row; basal cell bare; basal vein setose; speculum present, open posteriorly. Petiole (Fig. 20) longer than wide, with basal flange thickened laterally, without median carina, without lateral setae. Gaster of females lanceolate, length 1.6 or more times width; hypopygium extending $\frac{2}{3}$ length of gaster or more; in both sexes, hind margin of T1 sinuous laterally, emarginate medially (Figs 8, 21).

Discussion.—This genus is placed in the *Halticoptera*-group as defined in this paper by: the rounded pronotum, shallow notauli, undifferentiated frenum, propodeum with a median carina and plicae connected by a W-shaped carina, reticulate petiole with a complete basal flange, and T1 that is sinuous laterally and emarginate medially. *Mauleus* and *Halticoptera* exhibit considerable phenetic similarity. The clypeus of *Mauleus* is secondarily bidentate (Fig. 13); the left hand clypeal denticle is divided by a sulcus formed as a result of the near fusion of the two approximated left hand denticles. These denticles are shown in their plesiomorphic separated state in *Thinodytes* (Fig. 11). The same compound condition of the left denticle is found in *Halticoptera* Spinola (Heydon, unpublished data). [In contrast, in

the unrelated genus *Sphegigaster* Spinola, the left tooth in the bidentate clypeus is a single unit (Heydon, unpublished data)]. The compound clypeal denticular structure and the nonmetallic scape are possible evidence of a close phylogenetic relationship between *Halticoptera* and *Mauleus*. *Halticoptera* is well-defined cladistically relative to *Mauleus* by the very low insertion of the antennae (at or below the LOcL) and by the male maxilla, which has the terminal two segments of the palps flattened, expanded, and nearly always yellow and often the stipites also expanded. Two apomorphic characters readily define *Mauleus* relative to *Halticoptera* and related genera: 1. The propodeum is shortened in *Mauleus* (median panels over $2\times$ as wide as long in *Mauleus* species examined). 2. The basal flanges of the petiole are exceptionally large and thick, giving the petiole a connate appearance. The basal flanges in related genera are generally free-standing lamella and the petiole is more or less cylindrical.

Biology.—*Mauleus iligneus* has been reared from pupae of the native holly leaf miner, *Phytomyza ilicicola* Loew (Diptera: Agromyzidae). Like many other genera of the Miscogastrinae, it is likely that *Mauleus* species are parasitoids of the pupal stages of leaf-mining or stem-mining Diptera.

KEY TO DESCRIBED SPECIES OF *MAULEUS* GRAHAM

1. Pronotal collar with sides parallel in dorsal view (Fig. 23) 2
- Pronotal collar with sides widest near anterior margin and converging posteriorly in dorsal view (Figs 24, 25) 3
2. Vertex and mesoscutum with conspicuous pale setae. Propodeum with reticulations much less coarse than on scutellum, median panel each with broad shallow groove along anterior margin *nigritus* (Howard)
- Vertex and mesoscutum with indistinct dark setae. Propodeum with reticulations as coarse as on scutellum, median panel each with a pair of elongate sublateral depressions along anterior margin *maderensis* Graham
3. Propodeum with anterior depression between basal foveae; median panels with extensive area of weak, almost smooth sculpture. Pronotum with humeral angles acute, coming to blunt points in dorsal view (Fig. 25). MPP sensilla in two or more rows on funicular segments *venetus* Heydon
- Propodeum without distinct anterior depression between basal foveae; median panels almost entirely alveolate, with at most a small central patch of weak sculpturing. Pronotum with humeral angles either squared or slightly and smoothly convergent posteriorly (Fig. 24). MPP sensilla in single row on funicular segments (male of *M. cultratus* unknown) ... 4
4. Eye height 2.5–2.7× genal distance. Female with combined length of head and mesosoma longer than gaster; gaster less than twice as long as wide; hypopygium extending around $\frac{2}{3}$ gastral length (United States) *iligneus* Heydon
- Eye height 2.1–2.4× genal distance. Female with combined length of head and mesosoma less than or equal to length of gaster (Fig. 8); gaster more than twice as long as wide; hypopygium extending to near tip of gaster (southern México to Argentina) *cultratus* Heydon

Mauleus cultratus Heydon, **new species**

Fig. 8

Holotype, female.—Color: Head, pleural regions, propodeum dark blue; petiole bluish black; collar, dorsum of mesosoma greenish black; gaster dark brown, T1 with dark blue reflections. Antenna with scape brownish yellow with weak metallic reflections; pedicel, flagellum brown. Legs with coxae, trochanters, femora dark blue; tibiae brown except basal and apical tips brownish yellow; fore tarsi brown, middle and hind tarsi yellow-brown with pretarsi brown. Wing veins pale brown.

Sculpture: Clypeus, median portion of face finely alveolate; remainder of head, mesonotum, scutellum, frenum, median panels of propodeum alveolate; petiole finely alveolate; gaster smooth except T5–7 weakly coriaceous.

Structure: Body length (excluding ovipositor sheaths) 1.6 mm. Head width 1.2× height (26:21), 2.2× length (26:12); genal concavity extending $\frac{1}{3}$ malar distance; eye height 1.4× length (13.5:9.5), 2.2× malar distance (13.5:6.0), length 4.8× temple length; ratio of MOD, POL, OOL, LOL as 2:4:6:3; torulus 1X own diameter above LOcL. Antenna with length of pedicel plus flagellum 0.81× head width (21:26); ratio of lengths of scape, pedicel, annelli, F1–6, club as 9.0:3.5:1.0:1.5:2.0:2.0:2.0:2.0:5.0; widths of F1, F6, club as 2:3:3; MPP sparse, only one or two visible per segment from single view. Mesosoma length 1.4× width (33:23); pronotum with sides converging posteriorly; notauli incomplete; propodeum with width of median panels 2.2× length (11:5); basal fovea a shallow, triangular depression; plicae fading out in anterior $\frac{1}{2}$; spiracles 0.5× own diameter

from anterior margin of propodeum. Wing with relative lengths of submarginal, marginal, postmarginal, stigmal veins as 27:16:14:7; costal cell with single complete row of setae; basal vein setose with one seta posteriorly on cubital vein. Petiole length $1.5 \times$ width (9:6); sides narrowing posteriorly. Gaster lanceolate (Fig. 8), length $2.6 \times$ width (42:16), length $1.0 \times$ that of head and gaster (42:42); hypopygium reaching to apex of T7; ovipositor sheaths exerted for distance equal to half length of hind tibia.

Variation.—The color of the head, pleural regions, and petiole varies from dark blue, as in the holotype, to dark green and nearly concolorous with the dorsum of the mesosoma. The body length of specimens from the type locality is about 1.9 mm, whereas the length of the specimen from Ixtapan is 2.3 mm, the one from Morelia is 2.4 mm, and the female from Panamá is 3.1 mm in length. The ovipositor sheaths are exerted for a distance equal to $\frac{1}{3}$ to $\frac{1}{2}$ the length of the hind tibia.

Discussion.—*Mauleus cultratus* can be distinguished from *M. iligneus* by the characters given in the discussion section for that species.

Etymology.—The species name comes from the Latin word *cultratus*, meaning knife-shaped, and refers to the shape to the female gaster.

Type Material.—The holotype female (CNCI) and one paratype female were collected from San Cristóbal de las Casas, México, on 29 June 1969. Eight other paratype females were collected as follows (CASC, CDAE, CNCI, SEMC, USNM): Argentina. SALTA: Rosario de Lerma, 4-8.XI.1983 (Malaise trap). México. CHIA-PAS: San Cristóbal de las Casas, 1-12.V.1969; MICHOACAN: Morelia, 6.IX.1938; MEXICO: Ixtapan, 9.VII.1954; TAMAU-LIPAS: 6 miles n. Ciudad Victoria. Panamá. Chiriquí, XII.1946.

Biology.—The host(s) of this species are unknown.

Mauleus iligneus Heydon, new species
Figs. 13, 20, 21, 24

Holotype, female.—Color: Like that of *M. cultratus* except pedicel not metallic, and middle and hind tarsi white.

Sculpture. Clypeus and immediate vicinity finely alveolate (Fig. 13); remainder of head, mesoscutum, scutellum, frenum, median panels of propodeum alveolate; petiole finely alveolate; gaster smooth except T6 and T7 coriaceous.

Structure.—Body length 1.8 mm. Head width $1.3 \times$ height (29:23), $2.2 \times$ length (29:13); eye height $1.4 \times$ length (15.0:10.5), $2.5 \times$ malar distance (15:6), length $5.2 \times$ temple length (10.5:2.0); ratio of MOD, OOL, POL, LOL as 2.5:4.0:7.0:3.0; torulus located 1X own diameter above LOCL. Antenna with length of pedicel plus flagellum $0.88 \times$ head width (25.5:29.0); ratio of lengths of scape, pedicel, annelli, F1-6, club as 11.0:3.0:1.0:2.5:2.5:2.5:2.5:2.5:7.0; widths of F1, F6, club as 2.0:3.0:3.5. Mesosoma length $1.5 \times$ width (36.0:24.5); pronotum with humeral angles squared but sides convergent posteriorly (Fig. 24); notauli extending to hind margin of mesoscutum as impressed lines; propodeum (Fig. 20) with plicae fading out in anterior half, basal fovea extending halfway down median panels and bordered mesally by carina, nuchal area raised but acarinate anteriorly, spiracles almost on anterior margin of propodeum. Fore wing with relative lengths of submarginal, marginal, postmarginal, stigmal veins as 25:15:11:6; costal cell with one complete setal row and one partial row distally; basal vein with row of three setae. Petiole (Fig. 20) length $1.3 \times$ width (8:6); narrowing posteriorly; basal flanges large. Gaster fusiform (Fig. 21), length $0.87 \times$ length of head and mesosoma (39:45); length $1.8 \times$ width (39:22); hypopygium extending $\frac{2}{3}$ length of gaster; ovipositor sheath exerted for a distance equal to / length of hind tibia.

Allotype.—Male. Color similar to holotype except frons, callus green; flagellum

paler ventrally; tibiae brownish yellow. Body length 1.8 mm. Head with ocelli relatively larger, ratio of MOD, OOL, POL, LOL as 3.0:3.0:7.5:3.5. Antenna with lengths of pedicel plus flagellum $1.0 \times$ head width (31:31); relative lengths of scape, pedicel, annelli, F1–6, club as 10.0:3.5:1.0:3.0:3.5:3.0:3.0:3.0:8.0; widths of F1, F6, club as 2.5:3.0:3.0; setae reclinate. Gaster ovate, length $1.8 \times$ width (42:23) (Specimen critical-point dried so gaster in air-dried specimen will be shorter).

Variation.—Length of female specimens varies between 1.5 and 2.1 mm and males between 1.1 and 1.8 mm. Other than the rather large variation in size, this is a morphologically uniform species.

Discussion.—*Mauleus iligneus* differs from *M. cultratus* in the following: 1. The ratio of the eye height to the genal distance is more in *M. iligneus* [$\bar{x} = 2.56 \pm (\text{S.E.}) 0.022$ ($n=12$); range 2.5–2.7] than in *M. cultratus* [$\bar{x} = 2.24 \pm 0.038$ ($n=7$); range 2.1–2.4]. 2. *Mauleus iligneus* has a partial second row of setae in the costal cell of the fore wing, which is lacking from *M. cultratus*. 3. The ratio of the length of the head and mesosoma to the length of the gaster is relatively greater in *M. iligneus* [$\bar{x} = 1.23 \pm 0.03$ ($n=10$); range 1.2–1.4] (Fig. 21) than in *M. cultratus* [$\bar{x} = 0.918 \pm 0.035$ ($n=6$); range 0.8–1.0] (Fig. 8). 4. The ratio of the gastral length divided by its width is less for *M. iligneus* [$\bar{x} = 1.76 \pm 0.04$ ($n=10$); range 1.7–1.9] than for *M. cultratus* [$\bar{x} = 2.56 \pm 0.11$ ($n=6$); range 2.2–3.1]. 5. The hypopygium extends to about $\frac{2}{3}$ the length of the gaster in *M. iligneus* (Fig. 21), but is nearly even with the tip of T7 in *M. cultratus* (Fig. 8). 6. The ovipositor sheaths are exerted for a length equal to $\frac{1}{4}$ the length of the hind tibia in *M. iligneus* (Fig. 21), but for about $\frac{1}{3}$ to $\frac{1}{2}$ the length of the hind tibia in *M. cultratus* (Fig. 8).

Etymology.—The specific epithet for *Mauleus iligneus* is an adjective based on the Latin word *ilex*, meaning holly.

Type Material.—The holotype (USNM),

allotype (USNM), and an additional nine female and seventeen male paratypes (UCDC, USNM) were reared from *Phytomyza ilicicola* on *Ilex opaca* Solander at Lexington, Kentucky by D. A. Potter collected 16 May 1984. An additional 43 paratypes were collected as follows (CNCI, UCDC): ILLINOIS: Cave-in-Rock State Park, near Cave-in-Rock, 4.VI.1981, 1 female. KANSAS: Oswego, 17.V.1976, 1 female. MARYLAND: College Park, V.1954 (ex holly leaf miner) 1 male, VII–VIII.1937 (ex *Phytomyza ilicis*), 4 females, 8 males; Laurel, 14.V.1965, 1 female. NEW JERSEY: New Brunswick, 26.V.1947 (ex *Phytomyza ilicicola*), 1 female. TEXAS: Houston, 8.XII.1929 (ex leaf miner on *Ilex vomitoria* Solander), 1 female, 1 male; Sanderson, 9.V.1912, 1 female. VIRGINIA: Norfolk, V.1929 (ex *Phytomyza ilicis*), 2 females, 6 males; Richmond, V.1938 (ex *P. ilicis*), 10 females, 4 males.

Biology.—This species has been reared numerous times from the complex of *Phytomyza* mining the leaves of holly [Potter and Gordon 1985 (as *Sphegigaster* sp.), Underhill 1943 (as *Sphegigastrinae*, new genus, new species), and Langford and Cory 1936 (as *Sphegigaster* sp.)]. It may also be the species called *Halticoptera* sp. by Kulp (1968), but voucher specimens from Kulp have not been seen. Host records prior to 1968 are questionable because the *Phytomyza* complex on holly was not studied in detail until then (Kulp 1968).

Potter and Gordon (1985) reported that *Mauleus iligneus* was a primary parasite when its agromyzid host, the native holly leafminer, *Phytomyza ilicicola*, was unparasitized, but was a facultative hyperparasite on *Opius striativentris* Gahan (Hymenoptera: Braconidae) when that species had already parasitized the agromyzid maggot. Potter and Gordon reared no *Mauleus iligneus* from puparia collected just a few days prior to the emergence of *Phytomyza ilicicola* and speculate that *Mauleus iligneus* parasitizes the fly late in its pupal stage.

Mauleus maderensis Graham

Fig. 23

Mauleus maderensis Graham, 1981:8.

Holotype, female (BMNH) Hym. Type
No. 5.3454 (examined). Bouček and
Rasplus, 1991:41.

Diagnosis.—*Mauleus maderensis* differs from the three newly described species in that it has the sides of the pronotum in dorsal view as for most other Pteromalidae—more or less parallel, but weakly convex, with the broadest point being about halfway between its anterior and posterior edge (Fig. 23). The three new species of *Mauleus* described in this paper have the pronotum in dorsal view broadest near its anterior margin and distinctly convergent posteriorly. *Mauleus maderensis* is similar in propodeal structure to the Caribbean species *M. niritus*. However, these two species are easily distinguished by the characters given in the key.

Distribution.—Madeira (Pico das Arrudas, near São Martinho), and possibly Mexico (Bouček and Rasplus, 1991) because the species is associated with plants of Mexican origin (Bouček, pers. comm.).

Biology.—The insect host(s) of *M. maderensis* remain unknown.

Mauleus nigrinus (Howard),
new combination

Polycystus nigrinus Howard, 1897:142.
Holotype, female (BMNH); Hym. Type
No. 5.876 (examined). Heydon, 1989:193.

Diagnosis.—The type of *Mauleus nigrinus* is fragmented with most of the antennae gone and the gaster and petiole mounted on the card separately from the remainder of the body. Enough is remaining however, to confirm that this species belongs in *Mauleus*. *Mauleus nigrinus* differs from the three newly described species in that it has the sides of the pronotum in dorsal view more or less parallel, with the broadest point being about halfway between its anterior and posterior edge. The three new species of *Mauleus* described in this paper

have the pronotum in dorsal view broadest near its anterior margin and distinctly convergent posteriorly. *Mauleus nigrinus* is similar in pronotal structure to *M. maderensis*; however, these two species are easily distinguished by the characters given in the key.

Distribution.—*Mauleus nigrinus* is known to me only from the holotype collected at Baltazar, on the windward side of Grenada (West Indies) by H. H. Smith.

Biology.—The insect hosts of *M. nigrinus* remain unknown.

Mauleus venetus Heydon, **new species**

Fig. 25

Holotype, female.—Color: Body black except anterior aspect of head, collar, mesoscutum steel blue and lateral portions of metanotum, propodeum, T1 blue. Antenna with scape, ventral side of pedicel and F1 brownish yellow, remainder of pedicel and flagellum brown. Legs with coxae dark blue; femora brown with metallic blue reflections, except basal and apical tips brownish yellow; tibiae brownish yellow with weak brown bands mesally; tarsi white with pretarsi brown. Fore wing clear with veins brownish yellow, parastigma darker.

Sculpture.—Clypeus and immediate vicinity finely alveolate; remainder of head, mesoscutum, scutellum, frenum, median panels of propodeum alveolate; petiole finely alveolate; gaster smooth except T6 and T7 coriaceous.

Structure.—Body length 2.2 mm. Head width $1.4 \times$ height (42:30), $2.5 \times$ length (42.0:16.5); eye height $1.5 \times$ length (20:13), $2.0 \times$ malar distance (20:10), length $7.5 \times$ temple length (13:2); torulus $2 \times$ own diameter above LOC; ratio of MOD, OOL, POL, LOL as 3.0:6.5:9.0:4.0. Antenna with length of pedicel plus flagellum $0.90 \times$ head width (38:42); relative lengths of scape, pedicel, annelli, F1–6, club as 15.0:4.0:1.0:4.5:4.5:4.5:4.0:4.0:3.5:8.0; relative widths of F1, F6, club as 3.5:4.0:4.0; MPP sensilla in two rows on each flagellar seg-

ment; terminal club segment with small ventral patch of micropilosity. Mesosoma length $1.5 \times$ width (26.5:18.0); pronotum with humeral angles acute (Fig. 25); dorsellum short, anterior and posterior edges parallel; propodeum with region between basal foveae depressed (this depression shorter mesally than laterally and bounded posteriorly by weak carina), plicae fading out before reaching anterior margin of propodeum, nuchal region raised, margined anteriorly by carina, spiracles almost on anterior margin of propodeum. Fore wing with relative lengths of submarginal, marginal, postmarginal, stigmal veins as 37:23:15:8; costal cell with 1 complete and 1 distal partial row of setae; basal cell bare; basal vein with row of setae; speculum open posteriorly. Petiole length $1.1 \times$ width (9:8). Gaster length $1.4 \times$ width (43:31), $0.66 \times$ combined length of head and mesosoma (43:65); hypopygium extending about $\frac{1}{2}$ gastral length; ovipositor sheaths hardly extending beyond hind margin of T7.

Allotype, male.—Similar to female except: body length 1.8 mm. Head with ratio of MOD, OOL, POL, LOL as 3.5:4.0:7.0:3.0. Antenna with length of pedicel plus flagellum $1.1 \times$ head width (37:34); relative lengths of scape, pedicel, annelli, F1–6, club as 11.0:3.0:1.0:4.5:4.5:4.0:4.0:4.0:9.0; relative widths of F1, F6, club as 3.0:3.5:3.0; MPP sensilla numerous and distributed over funicular segments in many rows; setae reclinate, nearly absent. Gaster length $1.1 \times$ width (29:26).

Diagnosis.—*Mauleus venetus* is distinguished from the other two Nearctic *Mauleus* species by the acute humeral angles of the pronotum, the broad depression along the anterior margin of the propodeum, and the lack of sculpture over most of the median panels of the propodeum. *Mauleus venetus* most closely resembles *M. iligneus*—the coloration of the two species is almost identical except the propodeum is brighter blue in *M. venetus*. In addition, the MPP sensilla of *M. venetus* are ar-

ranged in two or more rows on each funicular segment in both sexes, whereas they are arranged in only one row in *M. iligneus*.

Etymology.—The species name comes from the Latin word *venetus*, meaning blue or sea-blue, and refers to the distinctive blue propodeum in this species.

Type Material.—The holotype (IRCW) is a female, collected in Grant Co. (T6N, R6W, S17), Wisconsin (USA), in a malaise trap exposed 7–14.VI.1976. The allotype (UCDC) was collected by the author on the South Farms of the University of Illinois, near Champaign, Illinois (USA) on 26.V.1985. Six paratypes were collected as follows (CNCI, IRCW, UCDC, USNM): Canada. QUEBEC: La Trappe, 12.VII.1942, 1 female. United States. ILLINOIS: University of Illinois South Farms, near Champaign, 26.V.1985, 1 male. MICHIGAN: Midland Co., 2.VII.1943, 1 male. VIRGINIA: Winchester, 16.VI.1964, 1 male. WISCONSIN: Grant, T6N, R6W, S17, 3–8.VI.1976 (gypsy moth Malaise trap), 1 female, 14–21.VI.1976 (gypsy moth Malaise trap), 1 female.

Biology.—The host(s) of *M. venetus* are unknown.

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**An Australian Masarine, *Rolandia angulata* (Richards)
(Hymenoptera: Vespidae): Nesting and Evaluation of
Association with *Goodenia* (Goodeniaceae)**

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Abstract.—An account is given of some aspects of the nesting of *Rolandia angulata* (Richards) (Masarinae). This wasp nests in multicellular burrows in compacted sandy soil. The sloping entrance to the burrow, not surmounted by a turret, is concealed beneath a pebble, a plantlet or a suitable item of debris. The main thrust of the shaft is vertically downwards, however, at intervals it curves outwards to end in a horizontal cell so that each cell, except the last excavated and therefore deepest one, appears to be accessed by a lateral shaft. The cells are unlined. The architecture of the nest and the method of its construction are discussed. The association between *Rolandia angulata* and *Goodenia* (Goodeniaceae) flowers, the source of nectar and pollen, is evaluated. It is shown that the association with *Goodenia pinnatifida* Schldl., at least, is mutually beneficial. Indeed it is suggested that in some areas, at some times, *R. angulata* may be the most important potential pollinator of this plant.

The genus *Rolandia* Richards, 1962 is listed by van der Vecht and Carpenter (1990) as a junior synonym of *Metaparagia* Meade-Waldo, 1911. As the analysis on which this is based has not yet been published the generic name *Rolandia* is used in the present paper. *Rolandia* is restricted to Australia. Four species are known, two, *R. maculata* (Meade-Waldo) and *R. houstoni* Snelling, from Western Australia, a third, *R. borrieriae* Snelling, from Northern Territory, and the fourth, *R. angulata* (Richards), the subject of this paper, from Queensland and New South Wales.

Rolandia angulata has been recorded from southwestern Queensland and northwestern New South Wales, from Cunnamulla [28.04S, 145.40E] (Richards 1968 as *Riekia angulata* and Snelling 1986) in the north to 90 km W of Cobar, Barnato Tanks [31.38S, 144.59E] (about 400 km south of Cunnamulla) (Richards 1968) in the south, and from three sites to the east of Cunnamulla, 80 km E of Cunnamulla (28.04S, 145.40E), 27 km W of St George

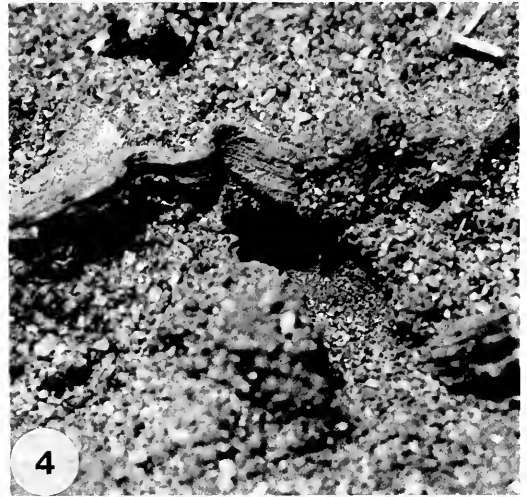
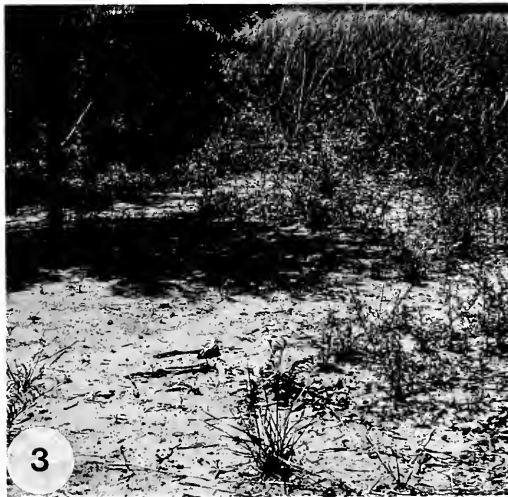
(28.03S, 148.30E), and 85 km E of St George (28.03S, 148.30E) (27–29.x.1993, F.W., S.K. and R.W. Gess).

There is only one published observation on the nesting of *Rolandia*—that of *R. maculata* entering a turretless, simple, oblique, blindly ending burrow in sandy ground (Houston, 1984). However, Houston is currently investigating further the nesting of this species and has made some details available for comparison.

The investigations concerning *R. angulata* published in the present paper were undertaken by the authors during the course of a fieldtrip to Australia in October 1993. Voucher specimens have been deposited in the Albany Museum (*R. angulata*, the forage plants, and the bee visitors to the forage plants), the Australian National Insect Collection, Canberra (*R. angulata*), and the Australian National Herbarium, Canberra (the forage plants).

NESTING

Description of the Nesting Areas.—Two nesting areas of *Rolandia angulata* were lo-



Figs. 1-4. 1, *Eucalyptus* woodland between St George and Cunnamulla, southwestern Queensland; 2, *Acacia* scrub 80 km east of Cunnamulla, southwestern Queensland; 3, a nesting site of *Rolandia angulata* 27 km west of St George, southwestern Queensland; 4, a nest entrance of *Rolandia angulata* beneath a piece of plant debris (approximately $\times 3.6$).

cated between St George and Cunnamulla in southern Queensland, one 27 km west of St George on 28 October and the other 80 km east of Cunnamulla on 29 October, the former in dry open woodland dominated by *Eucalyptus* (Fig. 1) and the latter in dry open scrub dominated by *Acacia* (Fig. 2). Both areas had recently received rain in the form of localized thundershowers which had resulted in a growth of annuals which were in flower on the road verges and in the low lying areas. The soil in both areas was sandy, compact but fri-

able. It was increasingly moist at least to the depth of the deepest nest cells, 38 cm.

Flowers Visited.—The only previous record of flower visiting by *R. angulata* is that of Richards (1968) for females collected on *Goodenia cycloptera* R.Br. in C.Sturt (Goodeniaceae) at Barnato Tanks. In the present study females and males were collected and observed visiting the yellow flowers of a prostrate herb also identified as *G. cycloptera* (Fig. 11) and an erect herb *Goodenia pinnatifida* Schldl. (Fig. 6) in the two areas where nests were discovered and

also in the area 85 km east of St George. At the most easterly site, that is 85 km east of St George, both species of *Goodenia* were common. Travelling westwards to Cunnamulla it was observed that *G. cycloptera* rapidly became uncommon whereas *G. pinnatifida* became increasingly common and at the site 80 km east of Cunnamulla was the most common roadside herb. The abundance of *R. angulata* followed a similar pattern to that of *G. pinnatifida*.

Visits to the flowers by female *R. angulata* were abundant by 10h00 and continued through the heat of the day and the afternoon. Visits became fewer in the late afternoon and ceased after 17h00. Males were observed to patrol the flowers and only later in the day to visit them for nectar.

All plants flowering together with the two *Goodenia* species, most notably several Asteraceae and a *Wahlenbergia* species (Campanulaceae), were sampled for flower visitors. None was being visited by *R. angulata*.

Provision.—Provision in the form of a firm, white pollen loaf was obtained from each of three cells. Pollen from the loaves was examined microscopically and found to match that obtained from the *Goodenia* flowers.

Mate location.—During the morning males patrolled the flowers where they sought the females. They did not alight on the flowers but rested on a neighbouring plant, for example on a grass stem, or on the ground. Numerous attempted copulations at flowers were observed and a single attempt to copulate with a nest-excavating female was noted. Several instances of a male and female grappling on the ground next to plants and of "hot pursuit" were noted.

Description of the Nest.—The nest ($n = 8$) consists of a subterranean burrow (Fig. 5) excavated in horizontal sandy soil in a clearing (Fig. 3). The entrance is concealed beneath a pebble, a plantlet or a suitable

item of debris (Fig. 4). It is a simple hole 3–4 mm in diameter, not surmounted by a superstructure. For approximately the first 10 mm the shaft slopes gently downwards. Thereafter its main thrust is vertically downwards, however, at intervals it curves outwards to end in a horizontal cell so that each cell, except the last excavated and therefore deepest one, appears to be accessed by a lateral shaft. These "lateral shafts" radiate out through 360° each deeper than that preceding it.

The diameter of the shaft narrows at a depth of approximately 80 mm and then continues constant. The first cell in the nests investigated was at a depth of between 180 and 370 mm, the "lateral shafts" were 30 mm in length, and the cells 13 mm long and 4 mm in diameter at the widest point. A lateral shaft is packed with sand after the cell which terminates it has been provisioned. Up to seven cells per nest were recorded. The cells are unlined.

Method of Construction of the Nest and Provisioning.—Water is not required for the excavation of the nest as the sandy soil, though compact, is friable. The sand extracted from the burrow is carried out of the shaft held between the head and the prosternum, the genae being fringed with ammochaetae. Whilst excavation is in progress, the female, when leaving the nest, backs out. During the initial stages of burrow excavation the extracted sand is dropped in flight in a more or less constant area to one side of the entrance and about 120 mm from it. As the burrow becomes deeper the extracted sand is dropped further from the nest in a constant arc about 250 mm from the entrance. The sand being scattered, there is no detectable accumulation and so no tumulus develops.

The presence of a recently hatched larva in a sealed, fully provisioned cell indicated that mass provisioning is practised. The sand used for packing a shaft leading to a cell is almost certainly obtained with-

in the nest during the excavation of the shaft leading to the next cell.

The fully fed larva spins a white cocoon which completely fills the cell. Like the sealed cell it is therefore rounded at the inner end and truncate at the outer end.

Discussion of Nesting.—The nest of *R. angulata* is essentially similar to that of *R. maculata*, which is described by Houston (pers. comm.) as a vertical burrow in sandy soil, about 300 mm deep and unlined, with unlined cells at the lower end. Thus the basic nest type for these two species of *Rolandia* can be defined as a multicellular sub-vertical burrow in horizontal ground excavated by the nester, without an entrance turret and with excavated cells not containing constructed cells. When compared with the seven basic nest types recognized for the Masarinae as a whole by Gess and Gess (1992) this appears to fit Nest type 1 except for the lack of an entrance turret. When the method of construction is compared with that of the species listed for this nest type, a basic difference is apparent. Water is used in the excavation and construction of Nests of type 1, like nests of types 2 and 3, whereas the nests of the two *Rolandia* species are excavated without the use of water. This is possible due to the friable nature of the soil in which they are sited. As noted in Gess and Gess (1992) nesting in friable soil in the Vespidae is probably derived rather than primitive as in the Pompilidae and Sphecidae. The nest type of the two *Rolandia* species is therefore seen as a sub-type which can be derived from Nest type 1.

Both species of *Rolandia* carry sand, extracted from the shaft, out of the burrow held between the head and the prosternum, the genae being fringed with am-

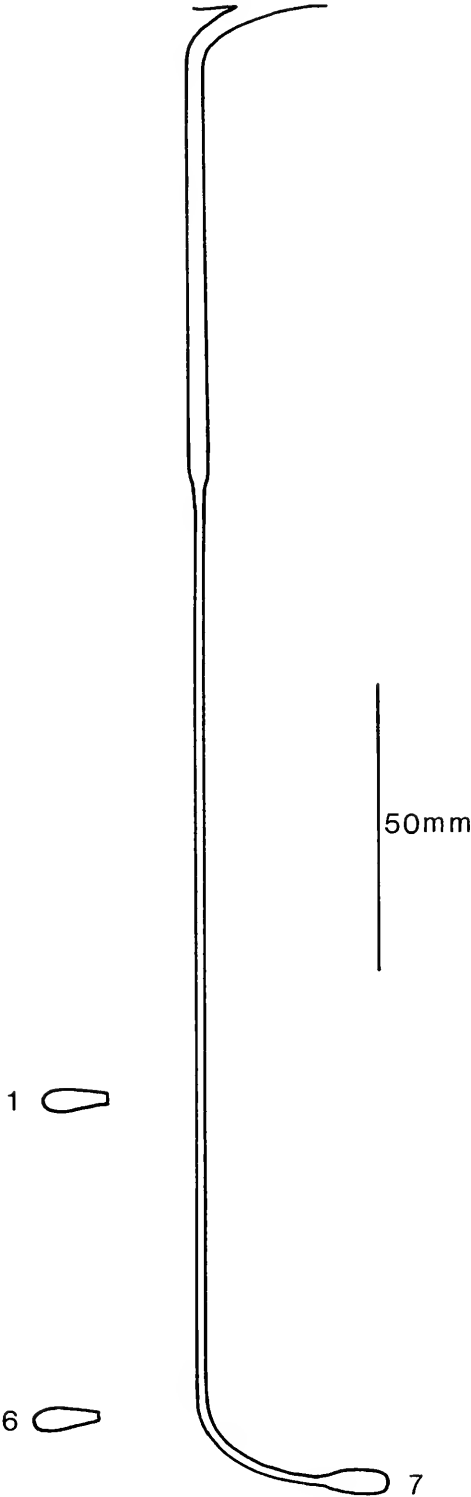


Fig. 5. Plan of vertical section of a nest of *Rolandia angulata*. Cells 2—5 followed cell 1, radiating out in sequence through 360° and at successively greater depths.



Figs. 6–10. 6, *Goodenia pinnatifida*, an erect herb; 7, a flower of *Goodenia pinnatifida*, indusium concealed by the bases of the adaxial petals; 8, *Rolandia angulata* entering a flower of *Goodenia pinnatifida*, indusium of the flower exposed ($\times 2.8$); 9, *Rolandia angulata* in nectar drinking position in a flower of *Goodenia pinnatifida*, indusium of the flower fitting snugly over the wasp's mesosoma ($\times 2.8$); 10, *Rolandia angulata* withdrawing from a flower of *Goodenia pinnatifida*, showing dusting of pollen on the head, dorsum of the prothorax, and anterior part of the mesoscutum ($\times 2.8$).

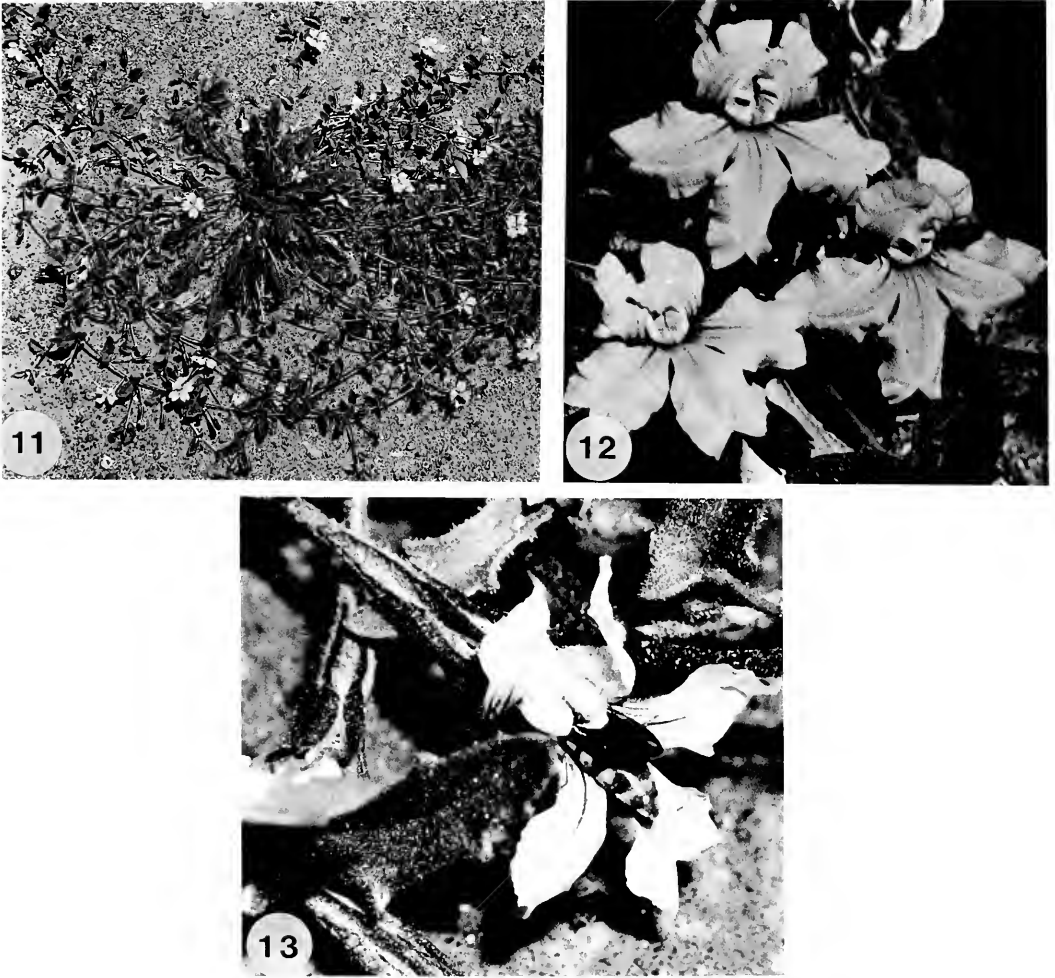
mochaetae. The possession of ammochaetae fringing the genae is a generic character (Snelling 1986) and it is therefore expected that all members of the genus excavate their nests in a similar manner. The only other vespid genus recorded as having a psammophore for the removal of the spoils of excavation is *Pterochilus* (Eumeninae) (Bohart 1940) for which nesting in vertical burrows in friable soil by two species has been described (Isely 1914 and Evans 1956).

EVALUATION OF ASSOCIATION WITH FLOWERS VISITED

Both *R. angulata* males and females obtain nectar and possibly pollen for their

own nourishment and females collect nectar and pollen for provisioning their nest-cells apparently solely from *Goodenia* flowers. They are therefore probably dependent on *Goodenia* flowers. To determine whether or not the association between the wasp and the flowers is mutually beneficial or not, that is whether or not the wasp in addition pollinates the flowers, requires a consideration of the functional morphology of the flowers, the behaviour of the wasps in the flowers, and wasp/flower fit.

Goodenia flowers are distinctly two lipped. The lower wings of the two ad-axial petals are differentiated in their lower parts into auricles which envelop the



Figs. 11–13. 11, *Goodenia cycloptera*, a prostrate herb; 12, three flowers of *Goodenia cycloptera*, indusium concealed by the bases of the adaxial petals; 13, *Rolandia angulata* in nectar drinking position in a flower of *Goodenia cycloptera*, indusium of the flower pressed down on the wasp's folded wings ($\times 3.3$).

indusium in the flower (Figs 7 and 12) so that it is only exposed when an insect visitor pushes the corolla lobes apart as it seeks the nectar at the base of the flower (Figs 8 and 13). The indusium is a cup at the top of the style and the surrounding stigmatic initial that collects and retains pollen from the stamens, which dehisce in the bud, and presents it thus to the pollen vector (Carolin, Rajput and Morrison 1992). Later the stigmatic initials mature and grow out of the indusium and collect pollen from pollen vectors.

R. angulata when visiting the flowers for nectar always alights on the lower lip and then pushes its way in beneath the indusium so that, if the flower is in the pollen presenting phase, the wasp receives pollen on its head. When it is in the nectar drinking position in a flower of *G. pinnatifida*, the mesosoma (Fig. 9) is snugly capped by the indusium but, when it is in a flower of *G. cycloptera*, which is deeper, it is the folded wings which are pressed beneath the indusium (Fig. 13). On emerging from a flower of *G. pinnatifida* it can be clearly

seen to have been well dusted with pollen not only on the head but also on the dorsum of the prothorax and the anterior part of the mesonotum (Fig. 10). When coming thus laden with pollen to a flower with receptive stigmas the wasp would be ideally suited to pollinate it. It is not clear, however, whether *R. angulata* would effectively pollinate the deeper flowers of *G. cycloptera*. It is possible that pollen may be transferred from its head to a receptive stigma but the pollen received on the wasp's wings is unlikely to be successfully transferred.

It is concluded that, within its limited distribution, *R. angulata* is a potential pollinator, at least, of the widespread species *G. pinnatifida* with which it therefore has a mutually beneficial association. However, at none of the sites was *R. angulata* the sole visitor to the *Goodenia* flowers.

At the most easterly site a second masarine, *Riekia nocatunga* Richards, which was also recorded from *Goodenia fascicularis* F.Muell. & Tate at Kondar to the southeast, was a relatively abundant visitor to *G. pinnatifida*. Furthermore the flowers of both species of *Goodenia*, particularly those of *G. cycloptera*, were visited abundantly by bees. The most common species was *Leioproctus* (*Chrysocolletes*) *moretonianus* (Cockerell) (Colletidae) which was also recorded from Goodeniaceae at several sites in Queensland by Michener (1965). Less common visitors were a second, but slightly smaller, species of *Leioproctus* (*Chrysocolletes*) and a species of *Megachile* (Megachilidae). Relatively uncommon visitors were six further species of *Megachile*, an additional colletid, a halictid, a few anthophorids and the honey-bee. Travelling westwards the bees were uncommon at the site 27 km west of St George and at the site 80 km east of Cunnamulla all but the second species of *Leioproctus* (*Chrysocolletes*) were absent. At the latter site a third much smaller species of *Leioproctus* was also recorded. However, *R. angulata* was the

only abundant visitor suggesting that in some areas, at some times, it may be the most important potential pollinator of *G. pinnatifida*.

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The following are thanked with appreciation: Terry Houston of the Western Australian Museum for permission to quote his unpublished observations concerning the nesting of *Rolandia maculata*; Jo Cardale of the Australian National Insect Collection, Canberra for facilitating the identification of forage plants; Kirsten Cowley, Australian National Herbarium, Canberra for the identifications of the forage plants; Alan Weaving of the Albany Museum for producing black and white negatives from the authors' colour transparencies for Figs 1-4 and 6-13; and the South African Foundation for Research Development for a rolling support grant to F.W.Gess, which made possible the fieldwork in Australia. The manuscript was reviewed by Karl V. Krombein and an anonymous reviewer, who are thanked for their constructive comments.

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Descriptions of the Male of *Riekia nocatunga* Richards, the Male and Two Strikingly Distinct Sympatric Colour Forms of *Riekia confluens* (Snelling) and the Male of *Rolandia angulata* (Richards) (Hymenoptera: Vespidae: Masarinae) from Australia

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Abstract.—The male of *Riekia nocatunga* Richards from southern Queensland, the male and two strikingly distinct sympatric colour forms of *Riekia confluens* (Snelling), comb. nov., from Western Australia, and the male of *Rolandia angulata* (Richards) from southern Queensland are described. The characters distinguishing *R. nocatunga* and *R. confluens* are discussed.

The Australian Masarinae and their natural history are relatively poorly known. During a recent collecting trip to Australia by the author, S.K.Gess and R.W.Gess, material collected included males of three species, *Riekia nocatunga* Richards, *Riekia confluens* (Snelling), comb. nov., and *Rolandia angulata* (Richards), hitherto described only from the female sex. Two strikingly distinct sympatric colour forms of *Riekia confluens* were found to occur. One of these was previously unknown and helps to elucidate the identity of a single male *Riekia* collected by T.F.Houston and discussed by Snelling (1986) who was unable to place it in a species.

Riekia Richards, 1962 and *Rolandia* Richards, 1962 have been sunk as junior subjective synonyms of *Metaparagia* Meade-Waldo, 1911 by van der Vecht and Carpenter (1990) on the basis of an as yet unpublished cladistic analysis by Carpenter. Until such time as this analysis is published and may be studied, the present author considers it best to continue to accept *Riekia* and *Rolandia* as genera in their own right.

Institutions in which the material studied is deposited are: Albany Museum,

Grahamstown, South Africa (AMG); Australian National Insect Collection, Canberra (ANIC); Western Australian Museum, Perth (WAM).

***Riekia nocatunga* Richards**

Riekia nocatunga Richards, 1962: 55–57, female.

This species was described from 7 miles N of Nocatunga [on maps as Nockatunga] [27.40S, 142.40E], Queensland (not New South Wales as in Richards 1962; correct in Richards 1968) (holotype female and 4 female paratypes) and Bourke [30.09S, 145.59E], New South Wales (1 female paratype).

Subsequently an additional five females from 90 km W of Cobar, Barnato Tanks [31.38S, 144.59E], New South Wales, were attributed to this species by Richards (1968). He noted that they differed from his original description with regard to the pale markings of which he gave some details. Two of these females, in the collection of the Natural History Museum, London, have been examined by the present author. They are confirmed as being *R. nocatunga*. They are less melanistic than the specimens originally described. The dark areas are less extensive and some, in par-

ticular those on the pronotum and tergites 1 and 2, are brownish rather than black. The light areas are more extensive and their colour is a strong yellow rather than pale lemon-yellow.

Snelling (1986) figured and briefly discussed a male *Riekia* from 43 km ENE Landor Homestead (25.08S, 116.54E) in Western Australia. Whereas it agreed generally with the original description of *R. nocatunga*, Snelling stated that there was no certainty that it was the opposite sex of that species and that he suspected that it was not. He listed some discrepancies, allowance being made for sexual differences, and stated that more material would have to be available before the specific status of the male could be determined.

Recently collected *Riekia* material, of relevance to the clarification of the above taxonomic question, consists of associated females and males from both Queensland and Western Australia. The specimens from Queensland are certainly *R. nocatunga*, as established by the comparison by the author of several of the females with the holotype in the Australian National Insect Collection, Canberra. The specimens from Western Australia on the other hand represent two strikingly distinct colour forms of *Riekia confluens*. One is superficially similar looking to *Riekia nocatunga* but morphologically distinct. The males of this form show the characters noted by Snelling for his male.

Male.—(Figs 3 and 4). Colour pattern very similar to that of female but differing in that the following parts are pale lemon-yellow: small streak on scapes distally, entire clypeus other than for narrow lateral and anterior margins, single large frontal spot between and above antennal sockets, narrow streak margining lower orbits, elongate spot in lower half of each ocular sinus (not rising above upper limit of frontal spot and separated from it by about width of antennal socket), uninterrupted but posteromedially narrowly emarginate pronotal band connecting humeri. Spot on

each side of mesoscutum where its furrows meet pronotum (usually but not always present in females) absent in both males examined.

Antennal scape (with radicle) very slightly longer than interantennal distance; first flagellomere less than half (0.4) as long as scape (with radicle), one and a third times as long as wide at its distal end, and one and one fifth as long as the second flagellomere. Last three flagellomeres flattened and slightly concave beneath; ultimate flagellomere narrowing apically and distinctly curved to form a hook.

Tergite 7 evenly rounded apically.

Genitalia (Figs 3 and 4); parameral spine broad and thick, evenly curved over its length and not hook-like apically; ventral process of each paramere relatively broad and short, subtriangular, without a narrow elongation; digitus short.

Length 7.5–7.8 mm; length of forewing 5.8 mm, hamuli 14.

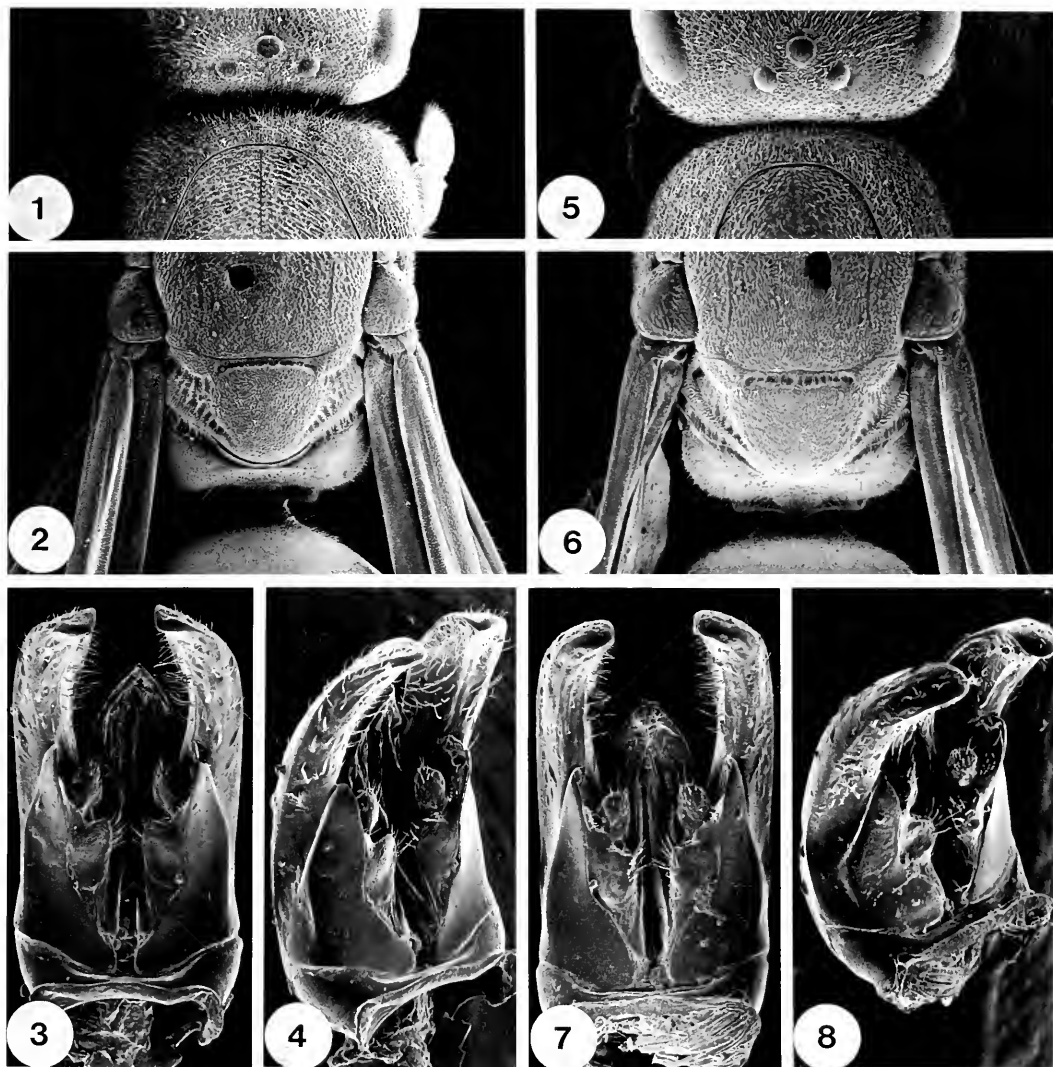
New Material Examined.—Queensland: Lundavra State School, Kondar (28.08S, 149.51E), 25.x.1993 (F.W., S.K. & R.W. Gess) 11 females, 1 male (in yellow flowers of *Goodenia fascicularis* F. Muell. & Tate, Goodeniaceae); Southwood Road, western boundary of Southwood National Park (27.56S, 149.30E), 26.x.1993 (F.W., S.K. & R.W. Gess) 2 females (at water); 85 km E of St George (28.03S, 148.30E), 27.x.1993 (F.W., S.K. & R.W. Gess) 8 females, 1 male (in yellow flowers of *Goodenia pinnatifida* Schldl., Goodeniaceae). Two females and 1 male in ANIC; 2 females in WAM; rest of material in AMG.

***Riekia confluens* (Snelling) comb. nov.**

Paragia confluens Snelling, 1986: 14 and Fig. 28, female.

Riekia sp. Snelling, 1986: 6, 8 and Figs 10, 19–21, male.

Snelling (1986) erroneously described *confluens* as a species of *Paragia* Shuckard, 1837 despite the fact that, in his own



Figs. 1-4. *Riekia nocatunga*. 1, dorsofrontal view of vertex and dorsal view of anterior third of thorax of female ($\times 17.6$); 2, dorsal view of posterior third of thorax of female ($\times 17.6$); 3-4, ventral and ventrolateral views of genitalia of male ($\times 57$).

Figs. 5-8. *Riekia confluens*. 5, dorsofrontal view of vertex and dorsal view of anterior third of thorax of female ($\times 17.6$); 6, dorsal view of posterior third of thorax of female ($\times 17.6$); 7-8, ventral and ventrolateral views of genitalia of male ($\times 63$); [all lemon-yellow colour form]

generic key, the species with its unconstricted gastral tergum 2 runs down to *Riekia* Richards, 1962. Further, with the exception of the number of spine-like setae at the apex of the mid- and hindtibiae (a specific character) the characters given by him in his diagnosis of the species are

all common to both *confluens* and *nocatunga* and may therefore be considered to be generic characters pertaining to *Riekia*. Similarly the confluence of the postocular and preoccipital carinae (leading to the name *confluens*), or alternatively the absence of the postocular ca-

rina, is a character shared with *nocatunga*. Conversely, the same characters set *confluens* (and *nocatunga*) generically apart from *Paragia*.

Material collected at a single site near Carnarvon, Western Australia, at distances of 165 km and 260 km in a westerly and west-south-westerly direction respectively from the type localities of *confluens* (16 km WSW Lyons River Homestead, 24.38S, 115.20E—paratype female, and 36 km ESE Minnie Creek Homestead, 24.00S, 115.42E—holotype female) consists of 53 females and 4 males. The material is divisible into two very distinct groups, one black and reddish-brown and the other black and lemon-yellow. Whereas intra-group variability is negligible, inter-group differences with respect to colour generally and to colour pattern on the metasoma in particular are striking.

The distinctness of the two sympatric groups and the notable absence of any intermediate forms initially led to the belief that two species were represented. However, no morphological characters could be found that supported this view and it is concluded that the apparent difference in overall facies is a product of the differences in colour and colour pattern. The reddish-brown colour form, consistent with the description of Snelling's two females (particularly with that of the paratype), is represented in the present material by females only, the lemon-yellow colour form by both sexes. To facilitate intra-specific comparison, descriptions limited to colour pattern are given of both female forms whereas for the purpose of inter-specific comparison with *nocatunga* the description of the male is given in greater detail.

In passing it is noted that in Snelling's description it is incorrectly stated that the probasitarsus is slightly more than twice wider than long. This is clearly an inadvertent error as it is in fact slightly less than half as wide as long.

Reddish-brown (RB) Colour Form

Female.—Black. The following reddish-brown: mandibles other than for teeth and extreme base, upper half of clypeal disc, a variously developed transverse band (seemingly formed of a pair of medially fused spots) between and above antennal sockets and narrowly separated ventrally (where sometimes angularly emarginate) from clypeal marking, variously sized elongate spot in upper half of each ocular sinus (rising to level of anterior ocellus and exceeding upper margin of frontal marking) [median frontal transverse band and lateral spots sometimes broadly fused above], a large oval spot behind eyes dorsally, entire upper surface of prothorax other than for narrow streak bordering posterior margin, tegulae except for clear testaceous central spot and narrow margin, scutellar disc other than for its anterior margin, a large spot on raised part of axillae and a minute spot between it and tegula, a diffuse spot on metanotum medially, a large spot on angles of propodeum, large spot on mesopleuron below tegula, distal end of mid- and hindcoxae, part of foretrochanter and whole of mid- and hindtrochanters, femur, tibia and tarsomeres of all legs, gastral tergite 1 other than for anterior declivity, tergite 2 other than for a variously developed anterior black band which may be triangularly produced in the middle and for a pair of widely separated diffuse dark markings on posterior margin, an anteriorly pointing triangular spot on posterior margin of tergite 3, tergite 4 other than for a narrow anterior black band, tergite 5, diffuse transverse posterior band on gastral sternites 2–5 (those of sternites 2 and 3 and sometimes 4 strongly and widely anteriorly produced in the middle).

Lemon-yellow (LY) Colour Form

Female.—(Figs 5 and 6). Black. The following reddish-brown: tip of mandibles except actual teeth, flagellomeres 1–10 be-

neath, trochanters of mid- and hindlegs, proximal half to three quarters of outer aspect of femora (where moderately to heavily black suffused) and inner and lower aspect of same, inner and lower aspect and distal end of tibiae, all tarsomeres, posterolateral portions of dark markings on sternites 2–4 and sternite 6 apically (all black-suffused). The following lemon-yellow: proximal half to two-thirds of mandibles, subapical spots on scapes, clypeus other than for narrow lateral and anterior margins and in some specimens arcuate black lines on distal half, a pair of irregularly shaped frontal spots between and above antennae, a narrow streak on lower inner orbits flanking clypeus, a broad mark in ocular sinus rising to level of anterior ocellus, an oval spot behind eyes dorsally, uninterrupted but posteromedially narrowly emarginate pronotal band connecting humeri, posterior corner of pronotum, tegulae except for clear testaceous central spot and narrow margin, a large transverse suboval shield-like spot on scutellum (not quite reaching anterior margin), a small spot on raised part of axillae, a large spot on angles of propodeum, large spot on mesopleuron below tegula, a small spot on mesosternum anterior to coxal cavities, a small lateral spot on mid- and hindcoxae, distal half of outer aspect of forefemora, distal spot on outer aspect of mid- and hindfemora, outer aspect of all tibiae (except distal ends), wide anteriorly trilobed posterior band on gastral tergites 1–5, tergite 6 (other than for variously developed posteriorly pointing V-shaped black mark leaving lateral and median spots or almost eliminating these), transverse posterior band on gastral sternites 2–5 (those of sternites 2 and 3 trilobed with median lobe strongly and widely anteriorly produced).

Male.—(Figs 7 and 8). Colour pattern very similar to that of female but differing in that the following parts are pale lemon-yellow: entire anterior aspect of scapes, entire clypeus other than for narrow lat-

eral and anterior margins, single large frontal spot between and above antennal sockets, lower aspects of mid- and hindcoxae, entire outer aspect of midfemora, entire outer aspect of all tibiae (including distal ends), narrow longitudinal streak on all basitarsi, transverse posterior band on gastral sternites 2–5 (all with median lobe strongly and widely anteriorly produced, together giving the effect of a wide median longitudinal band).

Antennal scape (with radicle) very slightly longer than interantennal distance; first flagellomere slightly more than half (0.53) as long as scape (with radicle), one and three quarter times as long as wide at its distal end, and twice as long as the second flagellomere. Last three flagellomeres flattened and slightly concave beneath; ultimate flagellomere narrowing apically and distinctly curved to form a hook.

Tergite 7 truncate and narrowly transverse apically.

Genitalia (Figs 7 and 8); similar to those of *R. nocatunga* but differing in detail particularly with respect to the form of the inwardly directed lobe of the volsella below the digitus.

Length 7.8–8.3 mm; length of forewing 5.5–5.7 mm; hamuli 12–13.

Material Examined.—Western Australia: 8 km NE of Carnarvon (24.51S, 113.45E) on road to Bibbawarra Bore, 3–5.x.1993 (F.W., S.K. & R.W. Gess) 16 RB females, 29 LY females and 4 LY males (in yellow flowers of *Lechenaultia* sp., Goodeniaceae), 4 RB females, 1 LY female (at water), 2 RB females, 1 LY female (without biological data). Two RB females, 2 LY females and 1 LY male in both ANIC and WAM; rest of material in AMG.

Discussion.—*R. confluens* may be distinguished from *R. nocatunga* in both sexes by the colour pattern and the below indicated morphological characters.

In *R. confluens* the ratio of POL (distance between posterior ocelli):OOL (distance between a posterior ocellus and nearest

eye margin) is 1:1.3–1.4, whereas in *R. nocatunga* it is 1:1.0–1.1.

In *R. confluens* the pilosity of the pronotum is only moderately dense, the individual hairs being slender and only slightly curved apically whereas in *R. nocatunga* the pilosity is much denser and the individual hairs are more robust and markedly and evenly curved.

In *R. confluens* the scutellum (Fig. 6) has its disc posteriorly widely and evenly to bluntly rounded and abruptly declivitous to the metanotum which it slightly overhangs; the posterolateral free edge of each lateral wing is almost straight. The metanotum in its median third is not depressed middorsally and is therefore of greatest depth in the middle; it is vertical, not visible from above. In *R. nocatunga* the scutellum (Fig. 2) has its disc posteriorly narrowly rounded and gradually descendant to metanotum which it does not overhang; the posterolateral free edge of each lateral wing is widely and shallowly concave. The metanotum in its median third is somewhat depressed middorsally and is therefore of even depth; it is sloping, visible from above.

In *R. confluens* gastral tergite 1 is two and two-fifths to two and a half times wider than long whereas in *R. nocatunga* it is two and a quarter times wider than long.

In *R. confluens* the number of spine-like setae on the apex of the mesotibia is 1 whereas in *R. nocatunga* it is 2–4, most commonly 3; the number of such setae on the apex of the metatibia is 1–2, most commonly 1, and 2–3 respectively.

The species differ in the female sex in the form of the pronotum as seen from above. In *R. confluens* (Fig. 5) the anterior and lateral margins describe a semicircle whereas in *R. nocatunga* (Fig. 1) the "shoulders" are anterolaterally produced so that the anterior and lateral margins do not describe a semicircle but the anterior margin appears subtransverse.

As may be seen from the descriptions,

the species differ in the male sex in the relative proportions of the first two flagellomeres, in the form of gastral tergite 7 and in slight differences in the genitalia.

Present data would indicate that the distributions of the species are widely separated, *R. nocatunga* occurring in New South Wales and Queensland and *R. confluens* in Western Australia.

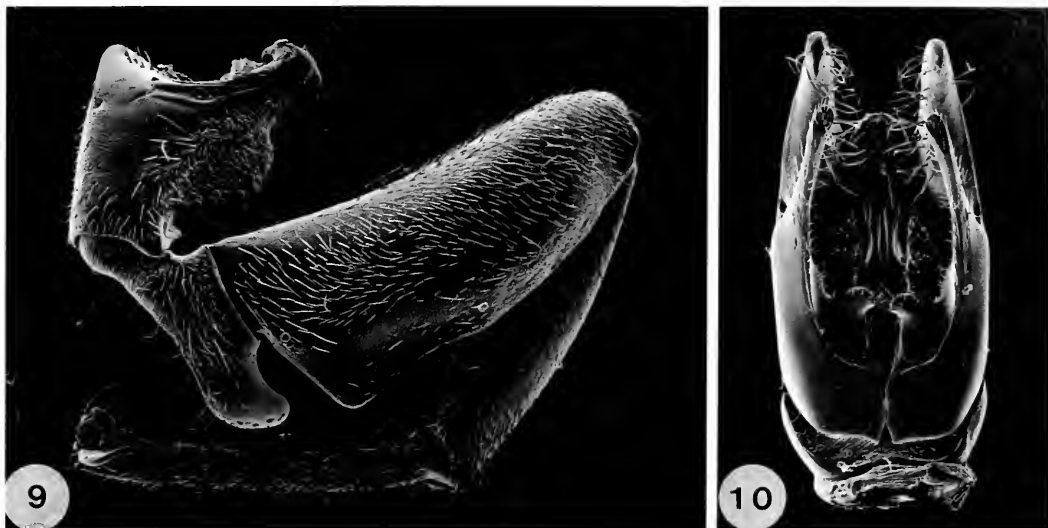
***Rolandia angulata* (Richards)**

Riekia angulata Richards, 1968: 101–102, female.
Rolandia angulata (Richards), Snelling, 1986: 8.

This species was described from Cunnamulla [28.04S, 145.40E], Queensland (holotype female and 1 female paratype) and from 90 km W of Cobar, Barnato Tanks [31.38S, 144.59E] (about 400 km south of Cunnamulla), New South Wales (12 female paratypes). Snelling (1986) recorded an additional 8 females from Cunnamulla. Hitherto the male appears to have been unknown. One of the present females was compared with the holotype in the Australian National Collection of Insects, Canberra, and found to be identical.

Male.—(Figs 9 and 10). Colour pattern very similar to that of female, differing chiefly in that the yellow markings are lighter in hue and brighter and contrast more strongly with the light reddish brown areas. The bright yellow mandibles, clypeus and transverse lower frontal marking, and the distinct median and lateral spots on the gaster facilitate recognition of the male even in the field.

Antennal scape (with radicle) shorter than interantennal distance; first flagellomere three times as long as broad at its distal end, about two-thirds as long as scape (with radicle) [three-quarters as long as scape without radicle], and a little more than twice as long as second flagellomere; flagellomeres 3–9 subequal in length and with the exception of 3 wider than long; 3–7 increasing in width; 7 and 8 of same width; 9 as wide as 6; 10 slightly longer



Figs. 9–10. *Rolandia angulata*. 9, posterior view of right fore leg of male ($\times 44.5$); 10, ventral view of genitalia of male ($\times 44.5$).

than preceding flagellomeres, narrowing and apically rounded; distal flagellomeres not modified beneath.

Foreleg (Fig. 9); process of foretrochanter large, compressed, broadly digitiform in posterior view and slightly forwardly curved, its apex attaining level of angulate base of forefemur; forefemur in posterior view broad and ventrally strongly angulate at base and widely but shallowly incurved from there to about midlength, with ventral margin angulate along its length but becoming lamellate at basal angle, with ventral surface basally (i.e. adjacent to lamellate ventral angle) excavated.

Genitalia (Fig. 10); parameral spines apically sharply pointed and ventrally recurved; ventral process of each paramere tapering towards apex in lateral view but in ventral view more or less of even width over most of its length and apically narrowly rounded; digitus and inwardly directed lobe of volsella as figured.

Length 8.7–9.2 mm; length of forewing 6.3–6.5 mm, hamuli 16–18.

Material Examined.—Queensland: 85 km E of St George (28.03S, 148.30E), 27.x.1993

(F.W., S.K. & R.W. Gess) 6 females (in yellow flowers of *Goodenia cycloptera* R.Br. in C. Sturt, Goodeniaceae), 7 females (in yellow flowers of *Goodenia pinnatifida* Schldl., Goodeniaceae); 27 km W of St George (28.03S, 148.30E), 28.x.1993 (F.W., S.K. & R.W. Gess) 31 females, 10 males (in yellow flowers of *Goodenia cycloptera* R.Br. in C. Sturt, Goodeniaceae), 1 female (in yellow flowers of *Goodenia pinnatifida* Schldl., Goodeniaceae), 2 females (nesting in sandy soil), 2 females, 3 males (without biological data); 80 km E of Cunnamulla (28.04S, 145.40E), 29.x.1993 (F.W., S.K. & R.W. Gess) 49 females, 31 males (in yellow flowers of *Goodenia pinnatifida* Schldl., Goodeniaceae), 4 females (nesting in sandy soil), 9 females, 2 males (without biological data). Three females and 3 males in ANIC; 3 females and 3 males in WAM; rest of material in AMG.

Discussion.—Snelling (1986) was correct in his assumption that the males of *R. angulata* would differ from those of the very similar *R. houstoni* in the same characters as do the females. Of particular note is the scutellum which in both sexes of *R. angulata* slopes evenly to the metanotum and

lacks a definite posterior face. The males run down satisfactorily in Snelling's key, allowance being made for the longer than broad second flagellomere.

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in question quite clearly does not belong. Gratitude to the South African Foundation for Research Development is expressed for a rolling support grant which made the field work in Australia possible.

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The Last Twenty Years of Parasitic Hymenoptera Karyology: An Update and Phylogenetic Implications

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Abstract.—A survey of karyological data in the parasitic Hymenoptera shows a considerable uniformity in chromosome numbers within higher taxonomic groupings, with most chalcidoids having $n = 5$ –6 and most cynipoids, ichneumonoids and those very few species of Diapriidae and Scelionidae examined to date having $n = 10$ –12. The Encyrtidae and Eurytomidae differ from other chalcidoids examined to date in having higher n values (8–11). The braconid subfamilies Aphidiinae ($n = 4$ –7), Charmontiinae ($n = 5$) and Exothecinae ($n = 6$) are shown to have lower values than do other braconids. New data are presented for 32 species, including the first records of chromosome numbers for the Eupelmidae, Bethyridae, Diapriidae, Ormyridae, the ichneumonid subfamilies Banchinae, Pimplinae, and Tryphoninae, and the braconid subfamilies Aphidiinae, Charmontinae, Doryctinae, Exothecinae, Macrocentrinae, Meteorinae, and Miracinae. Chromosome number data are discussed in relation to current views on Hymenoptera phylogeny.

INTRODUCTION

There has long been a tendency for taxonomists to ignore many potential sources of systematic evidence in favour of more traditional morphological, and nowadays molecular, data. Whilst this lack has not been ubiquitous amongst taxonomists, where it has occurred it may have been due to a number of reasons including lack of understanding of novel characters, lack of facilities for investigating them and lack of availability of information about such characters. In this respect, it is not surprising that chromosome number and other karyological features have played little role in considerations of hymenopteran phylogeny, and this is especially true for the parasitic families. Reasons for this are manifold. Hymenopteran chromosomes have traditionally been studied in immature stages in which dividing cells are common, but larvae of parasitic wasps are perhaps especially difficult to identify and obtain except when species are in culture. Recent developments in the study of hy-

menopteran chromosomes (Imai *et al.* 1988, Baldanza *et al.* 1991b), have opened the possibility of greatly expanding our knowledge of parasitic wasp karyology. Further, it is now possible to obtain good results working with adult tissues such as ovaries (Gokhman 1985, 1990a), and such protocols have allowed, for the first time, an examination of chromosome number and structure in natural populations.

Karyological studies have, nevertheless, played an important role in the systematics and species level taxonomy of various groups of the non-parasitic Hymenoptera including sawflies, ants, bees and social wasps (principally Polistinae) and these have been reviewed in detail elsewhere (see for example, Kerr 1972, Kerr and da Silveira 1972, Naito 1982, Imai *et al.* 1977, Moritz 1986, Pompolo and Takahashi 1987, 1990, Hoshiba, Matsuura and Imai 1989, Costa *et al.* 1993). Wide variation in n is well known among the ants (Formicidae) and ranges from 1 to 47 (Imai and Taylor 1989, Imai *et al.* 1990), but is modal at 11 (Imai *et al.* 1988). Indeed, the greater

part of this range can even be found within the single ant genus *Myrmecia*. However, within the parasitic Hymenoptera there appears to be rather more consistency, and for most families the observed range of variation is far narrower.

Outside of the Hymenoptera, both chromosome numbers, structure and size have all been found useful in phylogenetic reconstruction, usually but not exclusively in combination with other morphocharacters, and this has been particularly true of plant systematics. For example, George & Geethamma (1992) have recently proposed a phylogeny of jasmines based on chromosome numbers and assumed polyploidy events. Among the insects, chromosome numbers have been used extensively in the systematic treatment and phylogeny of the Hemiptera (Blackman 1980, Emeljanov & Kirillova 1989, 1991). Kuznetsova (1985), for example, has concluded that the homopteran subfamily Orgeriinae is monophyletic based on an autosomal fusion giving $2n=27$ (in males) compared with the plesiomorphic value of $2n=29$ (in males), and similarly that the tribe Almanini of the Orgeriinae is monophyletic on the basis of an autosome-sex chromosome fusion (giving $2n=26$).

In this paper we review the current state of knowledge of the karyology of parasitic wasps and, in addition, provide new data for approximately 32 taxa including the first records of chromosome numbers for the Eupelmidae, Bethyridae, Diapriidae, Ormyridae, the ichneumonid subfamilies Banchinae, Pimplinae, and Tryphoninae, and the braconid subfamilies Aphidiinae, Charmontinae, Doryctinae, Exothecinae, Macrocentrinae, Meteorinae, and Miracinae.

MATERIALS AND METHODS

New karyotypic data were obtained using ovarian tissues of adult wasps which were either collected from the wild at Silwood Park, Berkshire, U.K., during early September 1995, or obtained from labora-

tory cultures. Chromosome preparations were obtained according to the schedule described in Appendix I. Voucher specimens for Ichneumoninae are deposited in the collection of Moscow State University, those for other taxa are in the Natural History Museum, London.

RESULTS AND DISCUSSION

The last review of chromosome number in the parasitic Hymenoptera was by Crozier (1975) at which time values were known for only about twenty species (with data published before 1930 not included for the reason of insufficient reliability); his data are summarized in Figure 1. Since then, chromosomes of nearly 140 additional species have been studied (Gokhman 1994), and for this review we have investigated 32 more in order to help fill in a number of gaps and to confirm some previous findings. These data are presented in Table 1 and summarized in Figure 2. The great majority of published chromosome numbers come from studies on the ichneumonid subfamily Ichneumoninae by Gokhman (1985, 1987, 1989, 1990a, 1990b, 1991a, 1991b, 1993a), though they also include a substantial body of evidence especially relating to various families of Chalcidoidea. Within the better studied parasitoid families (i.e. Ichneumonidae, Cynipidae, Torymidae) chromosome numbers were found to be relatively stable, and were generally uniform at the generic level. This contrasts markedly with observations for many aculeate Hymenoptera which often show striking chromosomal variability even within genera (Imai and Taylor 1989, Imai et al. 1990).

The apparent bimodality in haploid number of parasitic Hymenoptera apparent in Crozier's small sample (Fig. 1) now appears to be well founded (Fig. 2). However, the exact modal numbers are slightly different ($n = 5$ and 11 compared with $n = 5$ and 10 of Crozier), probably due to the strong bias in favour of the ichneumo-

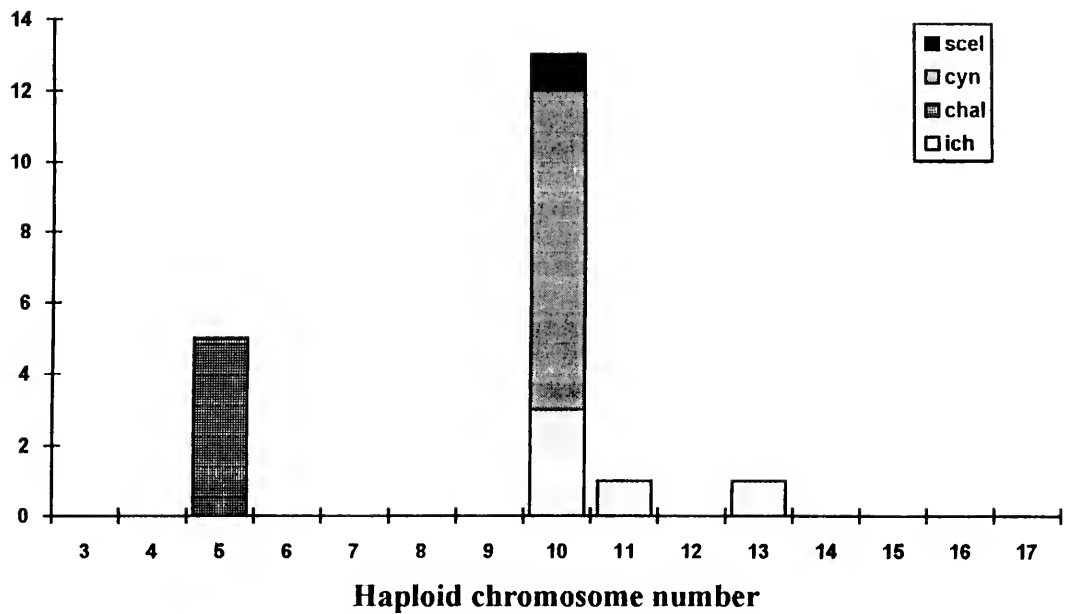


Fig. 1. Histogram of haploid chromosome numbers for parasitic Hymenoptera, data modified after Crozier (1975) to take into account subsequent taxonomic changes.

nid subfamily Ichneumoninae in the present enlarged data set. As will be apparent from the figures, the peak in haploid values around 5 largely comprises members of the Chalcidoidea and there is only slight overlap between these and the other peak centred around 11. The same is true, though less pronounced, when the data are plotted for genera rather than species (Figure 3: each *n* value in a genus being represented only once in the histogram). Members of three of the chalcidoid families investigated to date, the Eurytomidae (*Eurytoma*), Encyrtidae (6 species in three genera) and Aphelinidae (one species, *Pteroptrix* (= *Archenomus*) *orientalis* Silvestri, out of 5 investigated; see below) differ from other chalcidoids in having haploid numbers ranging between 8 and 11, whilst members of the braconid subfamilies Aphidiinae (*Aphidius*, *Diaretiella*, *Ephedrus*, *Praon*), Charmontinae (*Charmon*) and Exothecinae (*Rhysipolis*) are atypical in having haploid numbers of 4 to 7, 6 and 5 respectively, compared with other ichneu-

monoids whose haploid *n* values range from 8 to 17.

GENOMIC SIZE AND ITS IMPLICATIONS

Rasch *et al.* (1975, 1977) calculated the haploid genomic size of the braconid wasps, *Habrobracon juglandis* and *H. serinopae* both to be $0.15\text{--}0.16 \times 10^{-12}\text{g}$ DNA and that of the pteromalid, *Nasonia* (as *Mormoniella*) *vitripennis* to be $0.33\text{--}0.34 \times 10^{-12}\text{g}$. These values translate (using an average molecular weight of a base pair as 660) to base pair numbers of approximately 1.4×10^8 and 3.0×10^8 base pairs for the ichneumonoid and the chalcidoid respectively. More recently, Bigot *et al.* (1991) using DNA reassociation kinetics calculated the haploid genomic sizes of the ichneumonid *Diadromus pulchellus* and the chalcidoid, *Eupelmus vuilleti*, as $1\text{--}2 \times 10^9$ base pairs and 10×10^9 base pairs respectively. Unfortunately, no data for the numbers of chromosomes are available for *Eupelmus vuilleti* but we have investigated

Table 1. Chromosome number in parasitic wasps

| Taxon | n* | 2n* | Reference(s)† |
|---|-------|-------|---|
| Diaprioidea | | | |
| Diapriidae | | | |
| <i>Belyta depressa</i> Thomson | 8 | 16 | present paper†† |
| <i>Cinetus lanceolatus</i> Thomson | 10 | 20 | present paper |
| Scelionoidea | | | |
| Scelionidae | | | |
| <i>Telenomus fariai</i> Lima | 10 | 20 | Dreyfus & Breuer 1944 |
| Chalcidoidea | | | |
| Aphelinidae | | | |
| <i>Aphelinus mali</i> Haldeman | 5 | 10 | Viggiani 1967 |
| <i>Aphytis mytilaspidus</i> (Le Baron) | 5 | 10 | Rössler & De Bach 1973 |
| <i>Archenomus orientalis</i> Silvestri | 11 | 22 | Baldanza <i>et al.</i> 1991a |
| <i>Encarsia berlesei</i> Howard | 5 | 10 | Baldanza <i>et al.</i> 1991b |
| <i>Encarsia pergandiella</i> Howard | 6 | 12 | Hunter <i>et al.</i> 1993 |
| Chalcididae | | | |
| <i>Brachymeria intermedia</i> Nees | 3 | 6 | Hung 1986 |
| <i>B. lasus</i> Burks | 5 | 10 | Hung 1986 |
| <i>B. ovata</i> Say | 5 | 10 | Hung 1986 |
| <i>Dirhinus himalayanus</i> Westwood | 5 | 10 | Amalin <i>et al.</i> 1988 |
| Encyrtidae | | | |
| <i>Ageniaspis fuscicollis</i> Dalman | c. 10 | c. 20 | Silvestri 1908; Martin 1914 |
| <i>Copidosoma buyssoni</i> Mayr | 12 | 24 | Silvestri 1914 |
| <i>C. gelechia</i> Howard | 11 | 22 | Hegner 1915 |
| <i>C. gelechia</i> Howard | 10 | 20 | Patterson 1921 |
| <i>C. truncatellum</i> (Dalman) | 10 | 20 | Hunter & Bartlett 1975 |
| (= <i>?floridanum</i> Ashmead) | | | |
| <i>C. floridanum</i> Ashmead | 8 | 16 | Leiby 1922; Patterson 1917, 1921; Patterson & Porter 1917 |
| <i>C. floridanum</i> Ashmead | 11 | 22 | Strand & Ode 1990 |
| <i>Apoanagyrus lopezi</i> (DeSantis) | 10 | 20 | Dijken 1991 |
| Eulophidae | | | |
| <i>Cirrospilus diallus</i> Walker | 6 | 12 | present paper |
| <i>Colpoclypeus florus</i> Walker | 6 | 12 | Dijkstra 1986 |
| <i>Melittobia chalybii</i> Ashmead | 5 | 10 | Schmieder 1938 |
| <i>Tetrastichus gigas</i> Burks | 6 | 12 | Goodpasture 1974 |
| <i>T. megachilidis</i> Burks | 6 | 12 | Goodpasture 1974 |
| Eupelmidae | | | |
| <i>Anastatus catalonicus</i> Bolivar | 5 | 10 | present paper |
| <i>Macroneura vesicularis</i> (Retzius) | 5 | 10 | present paper |
| Eurytomidae | | | |
| <i>Eudecatoma biguttata</i> (Swederus) | 9 | 18 | present paper |
| <i>Eurytoma californica</i> Ashmead | 10 | 20 | Goodpasture 1974 |
| Leucospidae | | | |
| <i>Leucospis affinis</i> Say | 6 | 12 | Goodpasture 1974 |
| Ormyridae | | | |
| <i>Ormyrus</i> sp. | ?6 | ?12 | present paper |
| Pteromalidae | | | |
| <i>Anisopteromalus calandrae</i> (Howard) | 7 | 14 | present paper |
| <i>Coelopisthia extenta</i> (Walker) | 5 | 10 | present paper |
| <i>Dibrachys</i> sp. | 5 | 10 | Goodpasture 1974 |
| <i>Lariophagus distinguendus</i> Foerster | 5 | 10 | Gershenzon 1968 |
| <i>Muscidifurax zaraptor</i> Legner | 5 | 10 | Goodpasture 1974 |
| <i>Nasonia vitripennis</i> (Walker) | 5 | 10 | Gershenzon 1946, 1968; Pennypacker 1958; Whiting 1960, 1968; Wahr- man & Zhu 1993 |

Table 1. Continued

| Taxon | n* | 2n* | Reference(s)† |
|---|------------|--------|---|
| <i>Nasonia vitripennis</i> (Walker) | 5 + 0 – 1B | 10 | Nur <i>et al.</i> 1988; Werren 1991 |
| <i>Nasonia vitripennis</i> (Walker) | 6 | 12 | Goodpasture 1974 |
| <i>Pteromalus puparum</i> L. | 5 | 10 | Guhl & Dozortseva 1934, Dozortseva 1936 |
| <i>P. venustus</i> Walker | 5 | 10 | McDonald & Kronic 1971 |
| Torymidae | | | |
| <i>Monodontomerus clementi</i> Grissell | 6 | 12 | Grissell 1973b; Goodpasture 1975a |
| <i>M. montivagus</i> Ashmead | 6 | 12 | Goodpasture 1975a |
| <i>M. obscurus</i> (Westwood) | 4 | 8 | Goodpasture 1975a |
| <i>M. obscurus</i> (Westwood) | 6 | 12 | McDonald & Kronic 1971 |
| <i>M. saltuosus</i> Grissell | 5 | 10 | Grissell 1973b; Goodpasture 1975a |
| <i>Torymus baccharidis</i> Huber | 6 | 12 | Goodpasture & Grissell 1975 |
| <i>T. californicus</i> (Ashmead) | 6 | 12 | Goodpasture & Grissell 1975 |
| <i>T. capillaceus</i> Huber | 6 | 12 | Goodpasture & Grissell 1975 |
| <i>T. kochelei</i> Huber | 5 | 10 | Goodpasture & Grissell 1975 |
| <i>T. occidentalis</i> Huber | 6 | 12 | Goodpasture & Grissell 1975 |
| <i>T. tubicola</i> Osten-Sacken | 6 | 12 | Goodpasture & Grissell 1975 |
| <i>T. umbilicatus</i> Gahan | 5 | 10 | Goodpasture & Grissell 1975 |
| <i>T. vesiculi</i> Moser | 6 | 12 | Goodpasture & Grissell 1975 |
| <i>T. warreni</i> (Cockerell) | 6 | 12 | Goodpasture & Grissell 1975 |
| Trichogrammatidae | | | |
| <i>Trichogramma chilonis</i> Ischii | 5 | 10 | Hung 1982 |
| <i>T. deion</i> Pinto & Oatman | 5 | 10 | Stouthamer & Kazmer 1994 |
| <i>T. dendrolimi</i> Matsumura | 5 | 10 | Liu & Xiong 1988 |
| <i>T. evanescens</i> Westwood | 5 | 10 | Hung 1982 |
| <i>T. nubiale</i> Ertle & Davis | 5 | 10 | Hung 1982 |
| <i>T. pretiosum</i> Riley | 5 | 10 | Hung 1982; Stouthamer & Kazmer 1994 |
| <i>T. spp.</i> (7 strains) | 5 | 10 | Fukada & Takemura 1943 (cited by Hung 1982) |
| Cynipoidea | | | |
| Cynipidae | | | |
| <i>Andricus curvator</i> Hartig | 10 | 20 | Dodds 1938; Sanderson 1988 |
| <i>A. fecundator</i> Hartig | 10 | 20 | Dodds 1938 |
| <i>A. kollari</i> Hartig | 10 | 20 | Hogben 1920; Sanderson 1988 |
| <i>A. quercuscalicis</i> Burgsdorf | 10 | ?20 | Sanderson 1988 |
| <i>Aulacidea hieracii</i> Bouche | 10 | 20 | Dodds 1938 |
| <i>Biorrhiza pallida</i> Olivier | 10 | 20 | Dodds 1938 |
| <i>Callirhytis palmiformis</i> Ashmead | 10 | 20 | Goodpasture 1979b |
| <i>Cynips divisa</i> Hartig | 10 | 20 | Sanderson 1988 |
| <i>Diastrophus nebulosus</i> Osten-Sacken | 10 | 20 | Hegner 1915 ¹ |
| <i>Diplolepis elganteriae</i> Hartig | 9 | 27(3n) | Sanderson 1988 |
| <i>D. nervosum</i> Curtis | 9 | 18 | Sanderson 1988 |
| <i>D. rosae</i> L. | 9 | 18 | Henking 1892; Stille & Dävring 1980; Sanderson 1988 |
| <i>D. rosae</i> L. | ?12 | ?24 | Schleip 1909 |
| <i>D. spinosissimae</i> Girault | 9 | 18 | Sanderson 1988 |
| <i>Dryocosmus kuriphilus</i> Yasumatsu | 10 | 20 | Abe 1994 |
| <i>Dryophanta erinacea</i> Mayr | c. 12 | 24 | Wieman 1915 |
| <i>Neuroterus laeviunculus</i> Schenck | 10 | 20 | Sanderson 1988 |
| <i>N. numismalis</i> Fourcroy | 10 | 20 | Dodds 1938 |
| <i>N. quercusbaccarum</i> L. | 10 | 20 | Doncaster 1910, 1911, 1916; Dodds 1938 |
| <i>Trigonaspis megaptera</i> Panzer | 10 | 20 | Dodds 1938 |
| <i>Xestophanes potentillae</i> Retzius | 10 | 20 | Dodds 1938 |

Table 1. Continued

| Taxon | n* | 2n* | Reference(s)† |
|---|----|-------|---|
| Eucoilidae | | | |
| <i>Pseudeucoila bochei</i> Weld | 10 | 20 | Jungen cited in Crozier 1975 |
| Ichneumonoidea | | | |
| Braconidae | | | |
| <i>Aphidius rhopalosiphii</i> De Stefani Perez | 7 | 14 | present paper |
| <i>Biosteres carbonarius</i> (Nees) | 14 | 28 | present paper |
| <i>Charmon cruentatus</i> Haliday | 5 | 10 | present paper |
| <i>Cotesia glomeratus</i> (L.) (as <i>Apanteles</i>) | 12 | 24 | Hegner 1915 ¹ |
| <i>Dacnusa</i> sp. | 17 | 34 | present paper |
| <i>Diaeretiella rapae</i> McIntosh | 6 | 12 | present paper |
| <i>Ephedrus</i> sp. | ?7 | ?14 | present paper |
| <i>Habrobracon hebeter</i> Say | 10 | 20 | Torvik-Greb 1935 |
| <i>H. juglandis</i> Ashmead ² | 10 | c. 20 | Torvik-Greb 1935; Speicher 1937; Rasch <i>et al.</i> 1977 |
| <i>H. juglandis</i> Ashmead ² | 11 | 22 | Whiting 1927 |
| <i>H. pectinophorae</i> Watanabe | 10 | 20 | Inaba cited in Makino 1959 |
| <i>H. serinopae</i> Ramakrishna | 10 | 20 | Rasch <i>et al.</i> 1977 |
| <i>Heterospilus prosopidis</i> Viereck | 17 | 34 | present paper |
| <i>Macrocentrus thoracicus</i> (Nees) | 13 | 26 | present paper |
| <i>Meteorus versicolor</i> Wesmael | 8 | 16 | present paper |
| <i>Meteorus gyrator</i> Thunberg | 10 | 20 | present paper |
| <i>Meteorus pallipes</i> Wesmael | 10 | 20 | present paper |
| <i>Mirax</i> sp. | 10 | 20 | present paper |
| <i>Phaenocarpa persimilis</i> Papp | 17 | 34 | Prince & Stace (cited by Crozier 1977) |
| <i>Praon abjectum</i> Haliday | 4 | 8 | present paper |
| <i>Rhysipolis decorator</i> (Haliday) | 6 | 12 | present paper |
| Ichneumonidae | | | |
| <i>Aethercerus discolor</i> Wesmael | 11 | 22 | Gokhman 1985 |
| <i>Ae. dispar</i> Wesmael | 12 | 24 | Gokhman 1991 |
| <i>Ae. nitidus</i> Wesmael | 11 | 22 | Gokhman 1990a |
| <i>Ae. ranini</i> Gokhman | 11 | 22 | Gokhman 1991 |
| <i>Agrothereutes extrematus</i> (Cresson) | 10 | 20 | Koonz 1939 |
| <i>Aoplus pulchricornis</i> (Gravenhorst) | 13 | 26 | Gokhman 1990b |
| <i>Aptesis puncticollis</i> (Thomson) | 8 | 16 | Gokhman 1990a |
| <i>Baeosemus dentifer</i> Gokhman | 11 | 22 | Gokhman unpubl. obs. |
| <i>Baranisobas ridibundus</i> (Gravenhorst) | 11 | 22 | Gokhman 1990b |
| <i>Chasmodon motatorius</i> (Fabricius) | 17 | 34 | Gokhman 1985 |
| <i>Coelichneumon cyaniventris</i> (Gravenhorst) | 13 | 26 | Gokhman 1990a |
| <i>C. sugillatorius</i> (L.) | 13 | 26 | Gokhman 1990a |
| <i>Colpognathus celerator</i> (Gravenhorst) | 11 | 22 | Gokhman unpubl. obs. |
| <i>Cratichneumon viator</i> (Scopoli) | 14 | 28 | Gokhman 1985 |
| <i>Diadromus prosopius</i> Holmgren | 11 | 22 | Gokhman 1990a |
| <i>D. pulchellus</i> Wesmael | 11 | 22 | Hedderwick <i>et al.</i> 1985 |
| <i>D. subtilicornis</i> (Gravenhorst) | 11 | 22 | Gokhman 1990b |
| <i>D. troglodytes</i> (Gravenhorst) | 11 | 22 | Gokhman 1990a |
| <i>D. varicolor</i> Wesmael | 11 | 22 | Gokhman pers. obs. |
| <i>Dicaelotus</i> sp. nr. <i>parvulus</i> (Gravenhorst) | 11 | 22 | Gokhman 1990a |
| <i>D. pumilis</i> (Gravenhorst) | 11 | 22 | present paper |
| <i>Diphyus latebricola</i> (Wesmael) | 12 | 24 | Gokhman 1990a |
| <i>D. raptorius</i> (L.) | 12 | 24 | Gokhman 1990a |
| <i>Dirophanes callopus</i> (Wesmael) | 9 | 18 | Gokhman 1987 |
| <i>D. fulvitaris</i> (Wesmael) | 10 | 20 | Gokhman 1990a,b |
| <i>D. invisor</i> (Thunberg) | 10 | 20 | Gokhman 1987 |
| <i>Dyspetes arrogator</i> Heinrich | 10 | 20 | present paper |

Table 1. Continued

| Taxon | n* | 2n* | Reference(s)† |
|---|--------|---------------------|----------------------|
| <i>Ephialtes manifestator</i> (L.) | 15 | 30 | present paper |
| <i>Eurylabus torvus</i> Wesmael | 10 | 20 | Gokhman 1987 |
| <i>Gelis</i> sp. | 13 | 26 | present paper |
| <i>Glypta lapponica</i> Holmgren | 9 | 18 | present paper |
| <i>Heterischmus nigricollis</i> (Wesmael) | 11 | 22 | Gokhman 1990b |
| <i>H. truncator</i> (Fabricius) | 11 | 22 | Gokhman unpubl. obs. |
| <i>Homotherus locutor</i> (Thunberg) | 11 | 22 | Gokhman 1990b |
| <i>Ichneumon albiger</i> Wesmael | 12 | 24 | Gokhman 1990a |
| <i>I. amphibolus</i> Kriechbaumer | 12 | 24 | Gokhman 1990b |
| <i>I. bucculentus</i> Wesmael | 12 | 24 | Gokhman 1993a |
| <i>I. confusor</i> Gravenhorst | 12 | 24 | Gokhman 1985 |
| <i>I. crassifemur</i> Thomson | 12 | 24 | Gokhman 1985 |
| <i>I. croceipes</i> Wesmael | 12 | 24 | Gokhman 1990b |
| <i>I. extensorius</i> L. | 12, 13 | 24, 26 ³ | Gokhman 1993a |
| <i>I. cf. extensorius</i> L. | 11 | 22 | Gokhman 1990a |
| <i>I. formosus</i> Gravenhorst | 11 | 22 | Gokhman 1990a |
| <i>I. gracilentus</i> Wesmael | 12 | 24 (25) | Gokhman 1993a |
| <i>I. gracilicornis</i> Wesmael | 11 | 22 | Gokhman 1990a |
| <i>I. ingratus</i> Hellén | 12 | 24 | Gokhman 1990b |
| <i>I. inquinatus</i> Wesmael | 13 | 26 | Gokhman 1993a |
| <i>I. insidiosus</i> Wesmael | 12 | 24 | Gokhman 1990a |
| <i>I. lugens</i> Gravenhorst | 12 | 24 | Gokhman unpubl. obs. |
| <i>I. melanotis</i> Holmgren | 12 | 24 | Gokhman 1990a |
| <i>I. minutorius</i> Desvignes | 12 | 24 | Gokhman 1987 |
| <i>I. molitorius</i> L. | 12 | 24 | Gokhman 1990a |
| <i>I. nereni</i> Thomson | 11 | 22 | Gokhman 1990a |
| <i>I. sarcitorius</i> L. | 11 | 22 | Gokhman 1990a |
| <i>I. stramentarius</i> Gravenhorst | 12 | 24 | Gokhman 1987 |
| <i>I. submarginatus</i> Gravenhorst | 10 | 20 | Gokhman 1990a |
| <i>I. subquadratus</i> Thomson | 12 | 24 | Gokhman 1990b |
| <i>I. suspiciosus</i> Wesmael | 12 | 24 (26) | Gokhman 1993a |
| <i>I. validicornis</i> Holmgren | 12 | 24 | Gokhman unpubl. obs. |
| <i>Lissonota</i> sp. | 11 | 22 | present paper |
| <i>Mastrus smithii</i> (Packard) | 13 | 26 | Koonz 1936 |
| <i>Oronotus binotatus</i> (Gravenhorst) | 11 | 22 | Gokhman 1987 |
| <i>Orthocentrus</i> sp. | 14 | 28 | Gokhman 1990a |
| <i>Orthopelma mediator</i> (Thunberg) | 11 | 22 | Hogben 1920 |
| <i>Patrocloides chalybeatus</i> (Gravenhorst) | 8 | 16 | Gokhman 1993a |
| <i>Phaeogenes melanogonos</i> (Gmelin) | 11 | 22 | Gokhman 1990b |
| <i>Ph. nigridentis</i> Wesmael | 11 | 22 | Gokhman 1990b |
| <i>Ph. semivulpinus</i> (Gravenhorst) | 9 | 18 | Gokhman unpubl. obs. |
| <i>Ph. spiniger</i> (Gravenhorst) | 11 | 22 | Gokhman 1990a |
| <i>Polysphincta tuberosa</i> Gravenhorst | 9 | 18 | present paper |
| <i>Pseudoamblyteles homocerus</i> (Wesmael) | 9 | 18 | Gokhman unpubl. obs. |
| <i>Stenichneumon culpator</i> (Schrank) | 14 | 28 | Gokham 1985 |
| <i>Sycaonia sicaria</i> (Gravenhorst) | 11 | 22 | Gokham 1990b |
| <i>Syspasis alboguttata</i> (Gravenhorst) | 11 | 22 | Gokhman 1985 |
| <i>S. scutellator</i> (Gravenhorst) | 11 | 22 | Gokhman unpubl. obs. |
| <i>Tycherus australogeninus</i> Gokhman | 11 | 22 | Gokhman 1991 |
| <i>T. bellicornis</i> (Wesmael) | 10, 11 | 20 (21) | Gokhman 1989 |
| <i>T. dilleri</i> Ranin | 11 | 22 | Gokhman 1989 |
| <i>T. fuscicornis</i> (Wesmael) | 11 | 22 | Gokhman 1990b |
| <i>T. ischiomelinus</i> (Gravenhorst) | 9 | 18 | Gokhman 1991 |

Table 1. Continued

| Taxon | <i>n</i> * | 2 <i>n</i> * | Reference(s)† |
|--|------------|--------------|---------------|
| <i>T. ophthalmicus</i> (Wesmael) | 11 | 22 | Gokhman 1990a |
| <i>T. osculator</i> (Thunberg) | 11 | 22 | Gokhman 1989 |
| <i>T. suspicax</i> (Wesmael) | 11 | 22 | Gokhman 1987 |
| <i>Venturia canescens</i> (Gravenhorst) | 11 | 22 | Speicher 1937 |
| <i>Virgichneumon digrammus</i> (Gravenhorst) | 17 | 34 | Gokhman 1990a |
| <i>V. faunus</i> (Gravenhorst) | 11 | 22 | Gokhman 1990a |
| <i>Vulgichneumon saturatorius</i> (L.) | 9 | 18 | Gokhman 1987 |
| Chrysidoidea | | | |
| Bethylidae | | | |
| <i>Epyris niger</i> Westwood | 14 | 28 | present paper |
| <i>Laelius utilis</i> Cockerell | 10 | 20 | present paper |

* In papers which only quote *n* or 2*n*, the other value has been surmised and is given in italics.
† Data appearing in works before 1930 should be considered with great caution as most resulted from histological rather than cytological protocols, involving sectioned material rather than squash preparations and also often involving fixation techniques not well suited for the study of chromosomes, though some of these earlier findings are clearly correct including the oldest one (Henking 1892).
‡ For some new data we were not able to obtain an unambiguous chromosome number but our best approximation is presented (data indicated in table with a “?”) as in some cases these still provide potentially valuable information.
¹ Hegner (1915) did not provide a definitive statement on chromosome number and the data here come from his rather stylized figures; such data need therefore to be considered with extreme caution.
² Some workers consider *H. juglandis* to be a junior synonym of *H. hebetor*, however, this is not yet absolutely confirmed and therefore we prefer to keep these records separate.
³ A single, probably aneuploid, female specimen with 25 chromosomes has also been found.

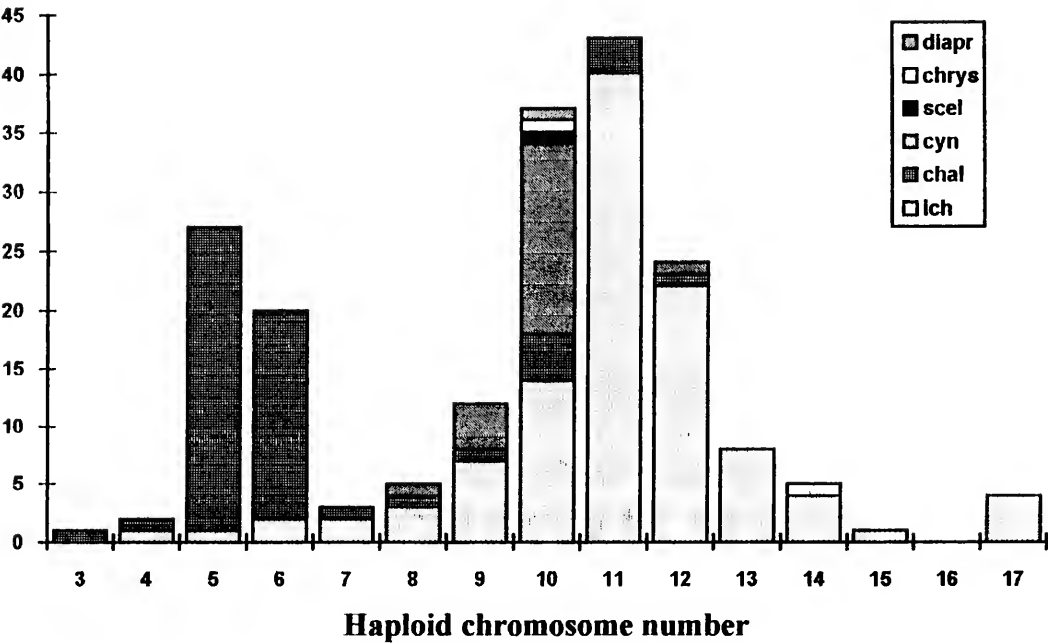


Fig. 2. Histogram of haploid chromosome numbers of parasitic Hymenoptera, data from Table 1 based on *n* values of each species.

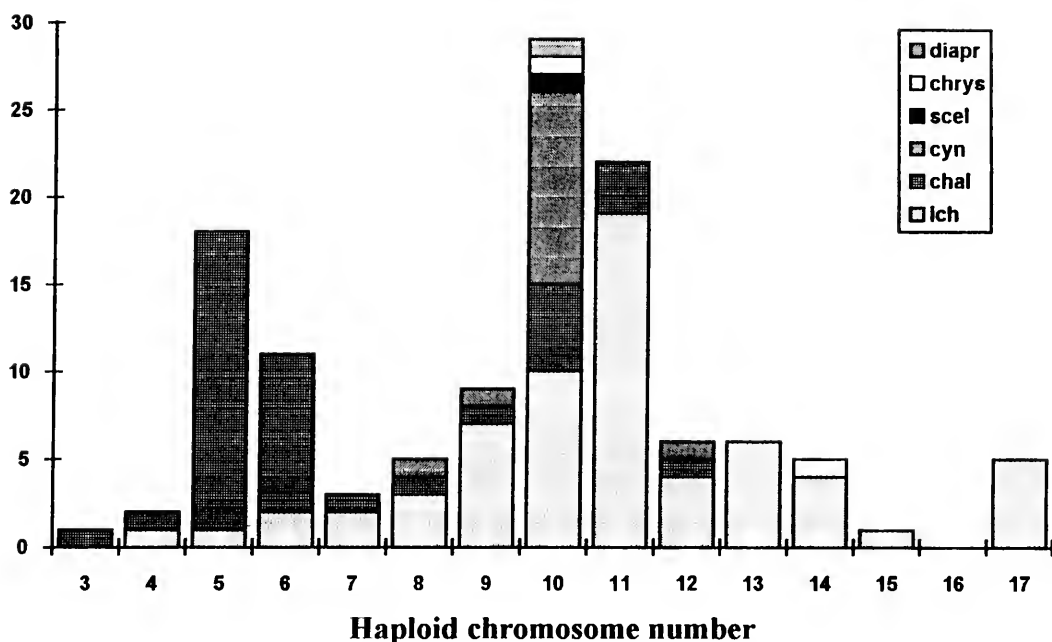


Fig. 3. Histogram of haploid chromosome numbers of parasitic Hymenoptera, data from Table 1, each *n* value occurring in a genus being represented only once.

two other eupelmid species in the genera *Macroneura* and *Anastatus*, which were both found to have haploid numbers of 5 in common with *Nasonia*. Although the results of Rasch *et al.* (1975, 1977) and of Bigot *et al.* (1991) don't quite agree in the order of magnitude of base pairs they estimate, probably due to differences in procedure, they did both show the chalcidoid to have a larger genome than the ichneumonid. Thus, if these values are roughly representative of other members of their superfamilies, then the chromosomes of most chalcidoids would be expected to have between four and twenty times as much DNA on average than chromosomes of ichneumonids.

CHROMOSOME NUMBER IN RELATION TO HYMENOPTERA PHYLOGENY

In karyological studies it is common practice to interpret modal chromosome numbers as representing the initial (ancestral) number, though to many cladists this

would be interpreted as the application of the much decried commonality principle. The 'common equals primitive' association is of course probabilistic rather than deterministic (Watrous and Wheeler 1981, Fröhlich 1987, Quicke 1993). Some further insight into whether modal chromosome number is likely to reflect the ancestral number can come from the comparison of modal and median numbers. If these numbers coincide, and the whole distribution may be approximated to a normal one, then the data provide no evidence of a directed change, though it must be remembered that there is always the possibility that an evolutionary change in chromosome number early in the evolution of the group could lead to the same distribution. In the Ichneumonoidea and the Cynipoidea both the median and modal chromosome numbers are the same 11 and 10 respectively; in contrast, for example, ants (Formicidae) have a modal number of 11 but the median is 15. However, cladistic analyses based on independent char-

acter systems, via outgroup comparisons, provide the most reliable means of determining plesiomorphic chromosome numbers and, where possible, this is the rational that we have employed.

According to currently accepted views of Hymenoptera phylogeny, the sawflies ('Symphyta') form a paraphyletic group with respect to the Apocrita with the latter being the sister group of the Orussidae, and the Apocrita+Orussidae in turn most probably being the sister group of the Xiphydriidae (Königsmann 1977, Rasnitsyn 1980, 1988, Gibson 1985). Unfortunately, chromosome numbers are not known either for the Orussidae or for the Xiphydriidae, although they are known for members of two other sawfly families with claims for a close relationship with the Apocrita, viz the Siricidae and Cephidae (Königsmann 1977, Basibuyuk & Quicke 1994, 1995). In the Cephidae n ranges from 9 to 22–26 (Mackay 1955, Crozier and Taschenberg 1972), whilst in the Siricidae, according to Sanderson (1932, 1970), the haploid number varies between 8 and 18. As regards other, less derived sawflies, haploid chromosome number ranges from 5 to 22 in the Tenthredinoidea, with three quarters of species having an n value ranging between 7 and 10 (Naito 1982). Taking the Siricidae and Cephidae as the two sawfly families closest to the ancestral lineage of the Apocrita (i.e. putative sister groups of the Apocrita + Orussidae) for which chromosome numbers are available, it seems reasonable to conclude that the plesiomorphic haploid chromosome number in the latter was at least 8 and possibly rather higher.

Within the Apocrita there is a picture emerging from independent investigations of phylogenetic relationships (Rasnitsyn 1988, Johnson 1988, Gibson 1985, Mason 1983, Quicke *et al.* 1993, 1994, Heraty *et al.* 1994) that the group divided relatively early in its history into a lineage giving rise to the Ichneumonoidea+Aculeata and a second comprising

the bulk of the taxa currently regarded as 'Microhymenoptera' including Chalcidoidea, Cynipoidea, Scelionoidea, Diaprioidea and Proctotrupeoidea s.s. (Fig. 4).

Our data show that the modal n value in the Ichneumonoidea, the probable sister group of the Aculeata, is 11. Further, our limited data for the less derived aculeates of the family Bethyridae (*Epyris* and *Laelius*; Fig. 10), whilst demonstrating some degree of variation in haploid number between 10 and 14, when considered together with data for other aculeates suggest the ancestral aculeate may have had a haploid number around 11, as was also concluded by Hoshiba, Matsuura and Imai (1989). Similarly, available values for three other parasitoid superfamilies, the Diaprioidea (Fig. 5), Scelionoidea and Cynipoidea, are similar. According to Rasnitsyn's (1988) phylogenetic hypothesis (see Fig. 4), the Scelionoidea are putatively the sister group of the Chalcidoidea s.l., and thus taking the former as the outgroup, the plesiomorphic haploid chromosome number for the Chalcidoidea may be postulated as being approximately 10. Therefore the data collectively support the hypothesis that the small values of n (from 3 to 7) found in the majority of Chalcidoidea are likely to be apomorphic. Unfortunately, there are no well founded views of relationships within the Chalcidoidea (Trjapitzin 1978, LaSalle 1987, Bouček 1988a, Woolley 1988, Noyes 1990, Gibson 1990), largely perhaps because of the considerable plasticity in adult morphology displayed by many of the families, which may result because of the undoubtedly polyphyletic natures of some family level taxa. Trjapitzin (1978) made few proposals about higher level relationships, and only suggested two possible groupings, his 'pteromaloid' group comprising Pteromalidae, Tanaostigmatidae, Eupelmidae and Encyrtidae, and a 'tetracampoid' group comprising Tetracampidae, Eulophidae, Elasmidae and Aphelinidae. A relationship between the Aphelinidae

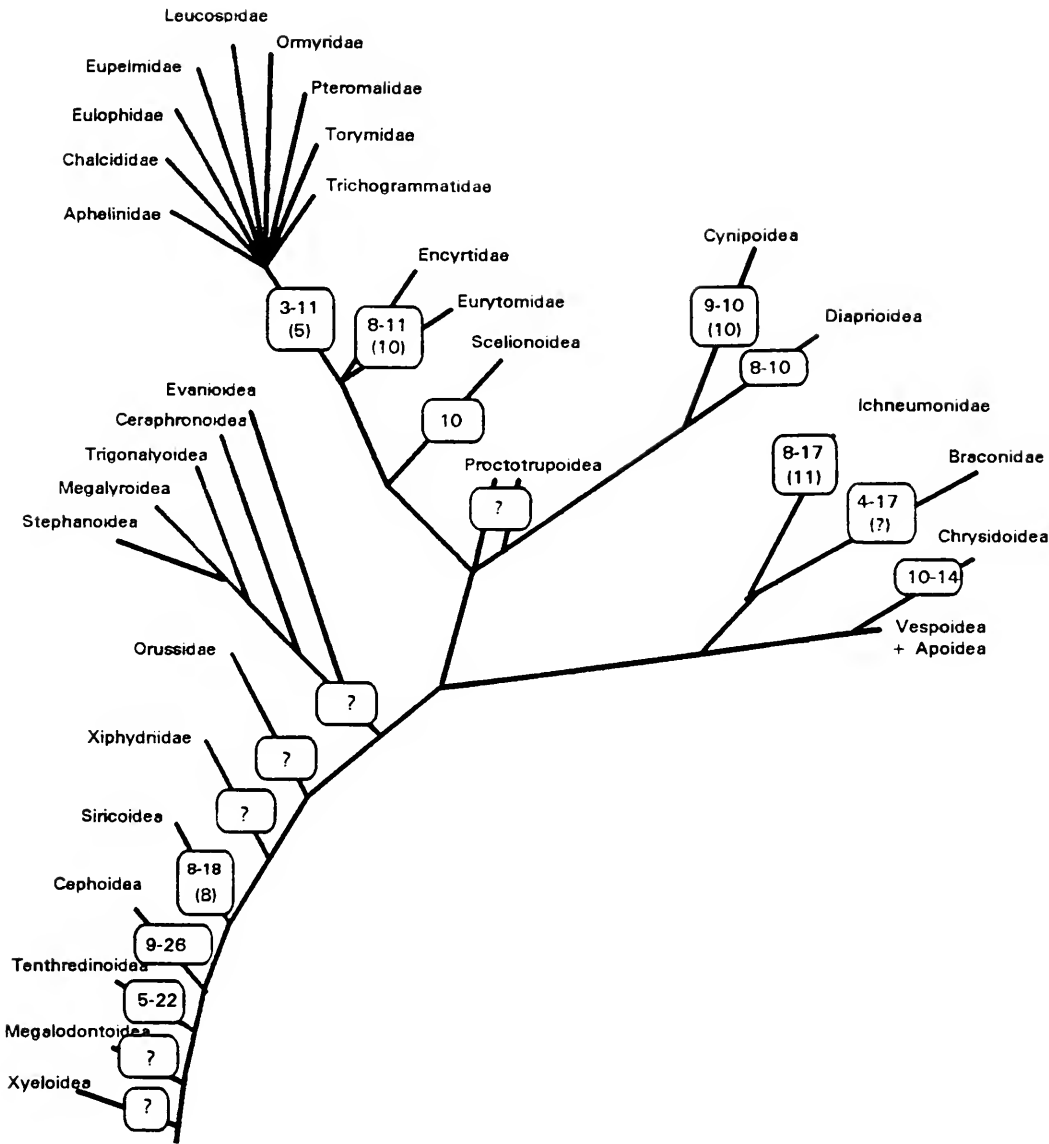


Fig. 4. Chromosome number and evolution of the parasitic Hymenoptera, with haploid values overlain on a cladogram in which superfamilial relationships are those proposed by Rasnitsyn (1988) but with relationships within the Chalcidoidea based on current karyological evidence for clarity. Ranges and (in parentheses) modal values.

and the Encyrtidae has also been proposed by a number of workers, but Gibson (1986) and Woolley (1988) considered that the supposed synapomorphies might be better regarded as resulting from convergence. LaSalle (1987) upheld Trjapitzin's view that the Tanaostigmatidae, Eu-

peimidae and Encyrtidae form a monophyletic group, citing two putative synapomorphies. Boucek (1988b) suggested that four families, the Chalcididae, Eurytomidae, Torymidae and [some] Pteromalidae were relatively 'ancient', partly because of their 5 segmented tarsi, compar-

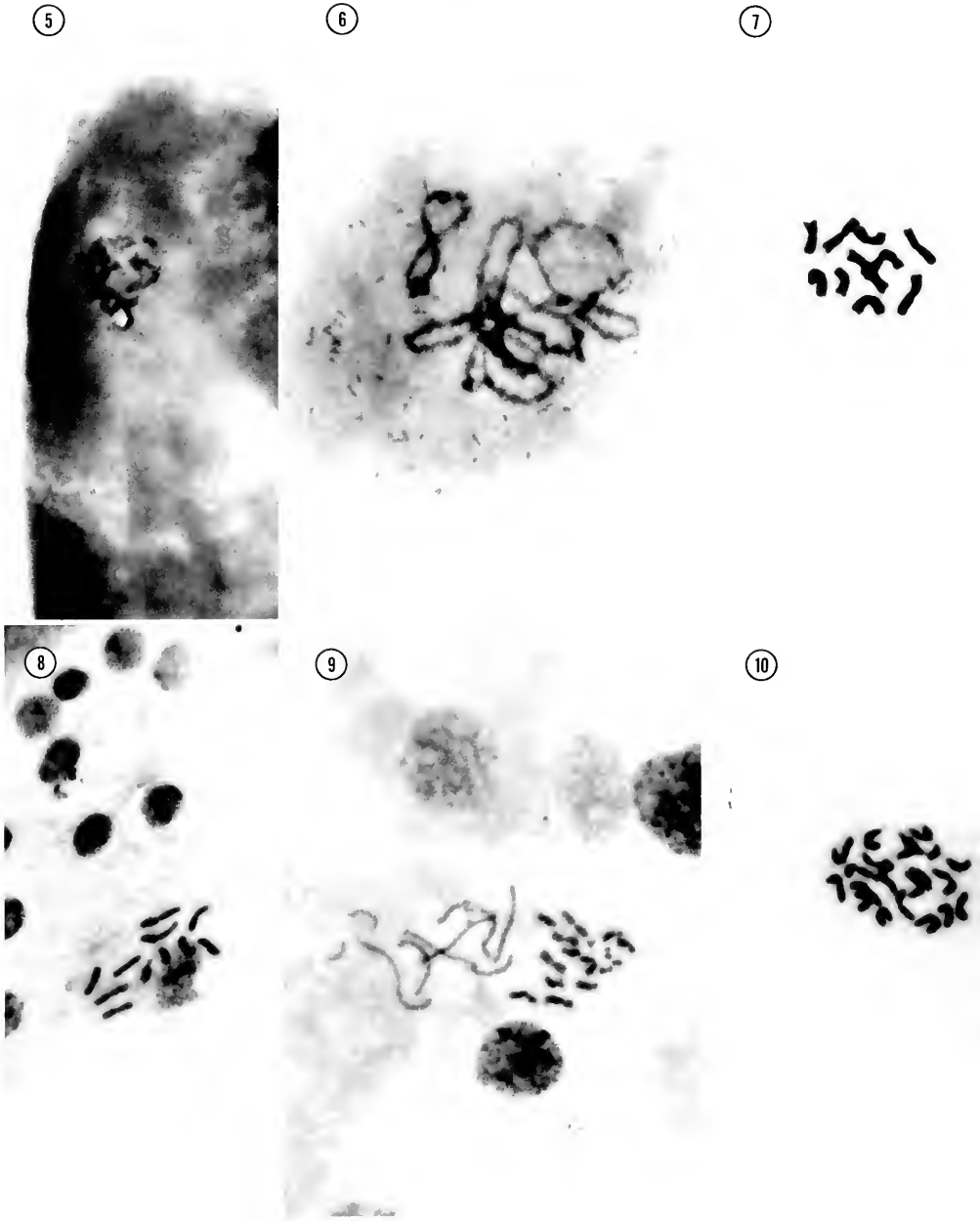


Fig. 5-10. Photomicrographs of chromosomes of adult female Hymenoptera revealed by Giemsa staining of ovarian tissue. 5, *Belyta depressa* (Diapriidae), meiosis, diakinesis in mature egg ($2n = 16$); 6, 7, *Anastatus catalonicus* (Eupelmidae), 6, meiosis, diplotene figures in developing oocyte, 7, metaphase mitosis ($2n = 10$); 8, *Diaretiella rapae* (Braconidae, Aphidiinae), metaphase mitosis ($2n = 12$); 9, *Meteorus versicolor* (Braconidae, Meteorinae), mitosis, one cell at pro-metaphase and one at metaphase ($2n = 16$); 10, *Laelius utilis* (Bethyliidae), metaphase mitosis ($2n = 20$).

atively large size and thoracic structure. and he agreed with Trjapitzin and LaSalle that at least the Eupelmidae and Encyrtidae might form a closely related group. However, this view was not supported by Gibson (1989, 1990) who considered both that the Eupelmidae might not be monophyletic and that the characters used to unite them with the Encyrtidae and Tanaostigmatidae are "... either primitive features or apparently were derived independently several times".

The present data could suggest that there has been an approximate halving of chromosome numbers within the Chalcidoidea, from around a modal number of 10 as shown by the Eurytomidae and Encyrtidae to 5 or 6 in Aphelinidae (but see below), Chalcididae, Eulophidae, Leucospidae, Ormyridae, Pteromalidae, Torymidae and Trichogrammatidae. It should be noted that within the Aphelinidae, whilst most taxa examined have haploid values of 5, *Pteropterix orientalis* has an n value of 11 (referred to as *Archenomus orientalis* by Baldanza *et al.* 1991a). However, *P. orientalis* is an highly derived species within the Coccophaginae, being either a sister group of *Coccophagoides* or representing a derived branch within *Encarsia* itself (A. Polaszek personal communication). In either case, the high haploid chromosome number in this taxon is clearly derived with respect to the values of 5 (and 6) displayed by the other aphelinids studied (collectively representing both the Coccophaginae and Aphelininae), and these lower values may therefore be taken as representing the ancestral range of values for the family as a whole. The n value of 11 in *Pteropterix orientalis*, being nearly twice that found in the other aphelinids investigated, is further suggestive that this taxon could have originated through a polyploidy event.

The karyological data summarized here lend some support to Boucek's view that the Eurytomidae are a relatively ancient and underived family of Chalcidoidea but

they do not agree well with the hypothesis of a close relationship between Eupelmidae and Encyrtidae (Trjapitzin 1978, LaSalle 1987, Boucek 1988a, Woolley 1988, Noyes 1990) which have haploid numbers of 5 (Figs 6, 7) and 8–11 respectively, because if a modal haploid chromosome number of 5 represents a synapomorphy, then this relationship would require either two separate reductions (from c. 10) or a reversal. However, a close relationship between Eupelmidae and Encyrtidae is not universally accepted (Gibson 1989, 1990), and chromosome number should be incorporated in future cladistic analyses of the superfamilies as an independent character.

Potentially significant variation occurs within the Braconidae and the Ichneumonidae. In the former family, several subfamilies have haploid numbers between 8 and 11, for example, the Braconinae (*Habrobracon*), Meteorinae (*Meteorus*; Fig. 9), and Miracinae (*Mirax*). However, rather higher numbers from 12 to 17 are found in the Doryctinae (*Heterospilus*), Alysiinae (*Phaenocarpa*, *Dacnusa*) and Opiinae (*Biosteres*), whereas substantially lower numbers ($n = 4$ to 7) are found in the Aphidiinae (*Aphidius*, *Diaretiella* (Fig. 8), *Ephedrus*, *Praon*), in the exothecine genus *Rhysipolis* ($n = 6$), and in the unrelated Charmontinae (*Charmon*; $n = 5$). The possession of low values within the four genera of Aphidiinae examined provides a potential synapomorphy for the group, which otherwise seems an heterogeneous assemblage in which members are united by few characters other than biology, and more taxa will need to be examined before this can be confirmed. The low n values found in *Rhysipolis* might be an autapomorphy, and it would be interesting to know something about chromosome numbers in the apparently closely related Clinocentrini and other Rogadinae s.s.. The haploid number of 5 found in *Charmon* was especially surprising as the subfamily seems to be close to the Macrocentrinae

(Quicke and Achterberg 1990, Quicke et al. 1994) for which we obtained a value of 13.

Within the Ichneumonidae, most data available up until now were for the subfamily Ichneumoninae but a few chromosome numbers for the Campopleginae (*Venturia*), Cryptinae (*Agrothereutes*, *Mastus*), Orthocentrinae (*Orthocentrus*), and Orthopelmatinae (*Orthopelma*) had also been published. The overwhelming majority of the species had haploid chromosome numbers modal at 11. We extended this data set by making chromosomal preparations also for the Banchinae (*Glypta*, *Lissonota*), Pimplinae (*Ephialtes* and *Polysphincta*), and Tryphoninae (*Dyspetes*). These additional data generally support the earlier findings, although the ephialtine genus *Ephialtes* had an n value of 15, rather higher than appears typical for the family, while the polysphinctine genus *Polysphincta* had the more typical, even low, haploid value of 9.

In addition to chromosome number, chromosome size and structure have been used extensively for cytotaxonomic purposes in other groups of organisms. Discussion of size and centromere position in the parasitic Hymenoptera is currently severely hampered by the relative paucity of data; in fact, in many illustrations, and especially among the earlier ones, centromeres are hardly (if at all) discernable. However, if we look at the karyotypes of the best studied groups (i.e. Ichneumonidae, Torymidae, Cynipidae), bi-armed (metacentric in the broad sense) chromosomes predominate in most cases (Figs 7–10). Some Hymenoptera, for example several *Diplolepis* species (Sanderson 1988), may also have numerous acrocentric chromosomes. Even less can be said about chromosome size, though in general in the parasitic Hymenoptera it is inversely related to chromosome number. Much more by way of comparative and quantitative data will have to be assembled before it will be possible to use these features to

any great extent in studies of Hymenoptera systematics.

INTRA- AND INTERSPECIFIC VARIATION AND IMPLICATIONS FOR HYMENOPTERA SYSTEMATICS

Only with the advent of techniques for examining chromosome number and morphology in adult Hymenoptera has it become possible to study intraspecific variation in nature and thus even to reveal the presence of hitherto unsuspected cryptic species or species complexes. As will be apparent from Table 1, chromosome number is often relatively consistent within a single genus. For example, in the Ichneumonidae, the 5 species of *Diadronus* for which chromosome numbers are available all have a haploid value of 11. Even for the large genus *Ichneumon*, 18 of the 25 species examined have $n = 12$.

Although chromosome numbers are usually considered as differentiating characters, serving to help distinguish between closely related forms, they may also be used in an integrative fashion, providing evidence for uniting related forms if the chromosome number represents a synapomorphy. For example, the discovery that all members of the cynipid genus *Diplolepis* have $n=9$, whereas the haploid values for all members of the other cynipid genera investigated to date for which reliable figures are available is 10, provides additional evidence for the monophyly of *Diplolepis*.

Chromosome numbers are fixed in the great majority of species of parasitic wasps whose populations have been studied in detail in the field. Two possible exceptions, however, are the ichneumonines *Ichneumon extensorius* and *I. suspiciosus*, both of which were revealed by Gokhman (1993a) to comprise individuals with two different diploid numbers, 24 and 26. Since specimens with the intermediate chromosome number were not found (with one possible exception in *I. extensorius*) the possibility that these represent

Table 2. Sibling species in the parasitic Hymenoptera detected by karyological features

| Family | Species | Chromosomal characteristics | Reference |
|---------------|--|-----------------------------|-----------------------------------|
| Ichneumonidae | <i>Aethecerus dispar</i> Wesmael | 2n = 24 | Gokhman 1991a |
| | <i>Aethecerus ranini</i> Gokhman | 2n = 22 | |
| Ichneumonidae | <i>Tycherus australogeminus</i> Gokhman | 2n = 22 | Gokhman 1991a |
| | <i>Tycherus ischiomelinus</i> (Gravenhorst) | 2n = 18 | |
| Ichneumonidae | <i>Ichneumon extensorius</i> L. | 2n = 24, 26 ¹ | Gokhman 1993a |
| Ichneumonidae | <i>Ichneumon suspiciosus</i> Wesmael | 2n = 24, 26 | Gokhamn 1993a |
| Encyrtidae | <i>Copidosoma "truncatellum</i> (Dalman)" ² | n = 10, 2n = 20 | Hunter & Bartlett 1975 |
| | <i>Copidosoma floridanum</i> (Ashmead) | n = 11, 2n = 22 | |
| | <i>C. floridanum</i> (Ashmead) | n = 8, 2n = 16 | |
| Pteromalidae | <i>Nasonia vitripennis</i> (Walker) | n = 5 + 0 - 1B, 2n = 10 | Nur <i>et al.</i> 1988 and others |
| | <i>Nasonia vitripennis</i> (Walker) | n = 6, 2n = 12 | |
| Torymidae | <i>Torymus californicus</i> (Ashmead) | n = 6(6M), 2n = 12 | Goodpasture & Grissell 1975 |
| | <i>Totrymnus warreni</i> (Cockerell) ³ | n = 6(5M + 1A), 2n = 12 | |
| Torymidae | <i>Monodontomerus obscurus</i> (Westwood) ⁴ | n = 4 | Goodpasture & Grissell 1975 |
| | <i>Monodontomerus obscurus</i> (Westwood) ⁴ | n = 6, 2n = 12 | |

Abbreviations: A = acrocentric; M = metacentric (in a broad sense).
¹ A single, probably aneuploid, female specimen with 25 chromosomes has also been found.
² Apparently belongs to *C. floridanum*.
³ Apart from *T. californicus*, the second chromosome pair in *T. warreni* has secondary constrictions.
⁴ Apparently belongs to *M. laticornis* Grissell & Zerova.

two sibling species rather than chromosomal races, seems much more likely, though the reverse cannot at present be discounted. Despite intensive effort, in neither case was it possible to detect any external morphological criteria to permit delineation of these putative taxa in the absense of karyological evidence. Further, in one instance, a chromosomal polymorphism in terms of C-banding pattern has been detected in the ichneumonine species, *Dirophanes invisor* (Thunberg). The C-banding patterns of the two homologous chromosomes of the second pair of metacentrics do not differ from one another in some individuals, but in others, this pair

is obviously heteromorphic, one member of the pair being substantially longer than the other, and its segment of pericentric heterochromatin is also much more developed (Gokhman 1993b). Several other recently discovered examples of apparent interspecific variation within other parasitic Hymenoptera are summarized in Table 2 and discussed below in more detail. The torymid chalcids *Torymus californicus* and *T. warreni* were considered to form a single species by Grissell (1973a). However, karyological analysis has shown that despite the fact that these two wasps have the same chromosome number (2n = 12), *T. warreni* has

a pair of acrocentric chromosomes and has secondary constrictions on the second largest pair of submetacentrics, whilst in *T. californicus* all the chromosomes are biarmed and the second pair has no constrictions (Goodpasture and Grissell 1975). Thus these two may well be best interpreted as sibling species. Other cases of possible karyologically-detected sibling species in the Chalcidoidea are more problematical. Goodpasture (1975a) and McDonald and Kronic (1971) reported $n = 4$ and $n = 6$ respectively for apparently the same torymid species, *Monodontomerus obscurus*. The most likely explanation for this difference is that one of these works involved a misidentified species with the specimens examined by McDonald and Kronic actually belonging to the very similar species, *M. laticornis* Grissell & Zerova, described 14 years later (Zerova and Grissell 1985). Two new ichneumonid species of the subfamily Ichneumoninae, *Tycherus australogeminus* and *Aethecerus ranini*, were originally detected on the basis of karyological evidence, but in each case reliable morphological differences were also found (Gokhman 1991a; see also Table 2).

Application of karyology may also be important in laboratory cultures as available evidence suggests that, at least in some instances, strains that were believed to belong to a single species may in fact represent more than one, with different laboratories working on different entities. For example, Hunter and Bartlett (1975) working with what they referred to as *Copidosoma truncatellum*, reported it as having a haploid number of 10. *C. truncatellum* was subsequently partly synonymized with *C. floridanum*, but Strand & Ode (1990) reported $n = 11$ for apparently the same species. Several earlier workers had reported the haploid number for *C. floridanum* (as *Paracopidosomopsis floridanus*) to be 8 (Leiby 1922, Patterson 1917, 1921, Patterson and Porter 1917), but their findings have to be treated with considerable caution as the techniques for fixa-

tion and preparation used in pre-1930 studies are often unreliable. Also in the genus *Copidosoma*, Hegner (1915) reported $n = 11$ and Patterson (1921) reported $n = 10$ for *C. gelechia*. Again these data may not be fully reliable for technical reasons. However, it is harder to interpret the apparent conflict in reported numbers for the widely studied pteromalid, *Nasonia vitripennis*. Many workers (e.g. Gershenzon 1946, 1968, Pennypacker 1958, Whiting 1960, 1968) have reported an n value of 5, but Goodpasture (1974) working on the University of California at Davis culture found $n = 6$. As with the case of the ichneumonines discussed below, intensive morphological investigation of these and other strains by Goodpasture failed to reveal any differences. Therefore, the possibility that the Davis culture had developed as a unique chromosomal race must be considered. Such variants are not uncommon in cultures of other organisms. However, it should be noted that Darling and Werren (1990) recently discovered two cryptic species of *Nasonia* in North America, and the karyological results could also reflect a sibling species complex.

The discovery of sibling species that can only reliably be separated by karyotype may pose a considerable nomenclatural problem, since the current Code of the Zoological Nomenclature requires new taxa to be differentiated from existing ones. As it is not normally possible to obtain karyological data from the type specimens of the species that have already been described, it would not be possible to give scientific names to both of them (Gokhman 1993a) unless it were possible (for instance through geographic distribution) to infer the karyotype of the described taxon.

Intraspecific karyotypic variation may also be of interest for population cytogenetics. This type of variation is favoured in Hymenoptera by some characteristics of their genetic system, which allows the sur-

vival and comparatively high viability of aneuploids (Imai *et al.* 1984). The data obtained, for example, for the ichneumonid *Tycherus bellicornis* suggest the long-term persistence of a chromosomal population polymorphism, probably induced by a translocation and subsequent non-disjunction of chromosomes (Gokhman 1989). Occasional aneuploid specimens were also found in *Ichneumon extensorius* and *I. gracilentus*. Perhaps the most interesting case of numerical chromosomal polymorphism is described by Nur *et al.* (1988) and Werren (1991) and occurs in the pteromalid, *Nasonia vitripennis*. This type of polymorphism implies the existence of a particular B chromosome. Being transmitted paternally into the diploid zygotes, this chromosome eliminates all other chromosomes of the paternal set from the zygote, thus converting the originally diploid zygote into a haploid one. Therefore this B chromosome may be considered as the most selfish genetic element ever known.

FUNCTIONAL IMPLICATIONS

Reduced chromosome numbers will generally be associated with reduced levels of recombination (Vorontsov 1966, White 1973). Under many circumstances, a reduction in recombination will be maladaptive. However, situations that favour high levels of inbreeding, for example, either parasitisation of aggregated hosts or gregarious parasitism combined with mating near the emergence site, may lead to selection in favour of low intrinsic levels of genetic diversity. Such situations may, for example, favour parthenogenesis or in the case of the parasitic Hymenoptera, thelytoky. Similarly, under such circumstances, high levels of recombination, or large numbers of separate linkage groups, will not be favoured, and consequently, mutations leading to reduced recombination will not necessarily be so deleterious. Such circumstances will permit a reduction in chromosome number more readily than will situations favouring high levels

of genetic diversity. Consideration of the data currently available for parasitic Hymenoptera may be relevant in this respect. For example, in the Aphidiinae the chromosome number is markedly lower than in the rest of the Braconidae. Aphidiines parasitise aphids which in turn often form clonal patches. In chalcidoids, many species are also gregarious or attack clustered hosts, perhaps in part as a result of their small size and dispersal capabilities. It would be difficult to quantify this, but the possibility exists that inbreeding may be more common in the Chalcidoidea as a whole than in the Ichneumonoidea or Cynipoidea (Askew 1968). Information on recombination levels in parasitic Hymenoptera is extremely limited to date (Crozier, 1975), being based on linkage data (*Habrobracon hebetor*) and chiasmata per bivalent arm (*Aphytis mytilaspidus*). Further studies taking into account cross-over and levels of heterozygosity in parasitic wasps with different biologies and different chromosome numbers and morphologies might provide additional evidence in this respect.

FURTHER PERSPECTIVES

Though we have managed for the first time to obtain cytogenetic information for several major groups of parasitic Hymenoptera, the overwhelming majority of these insects still remains untouched by karyological investigation, and this includes some entire superfamilies such as the Stephanoidea, Megalyroidea, Trigonalyoidea, Evanioidea and Ceraphronoidea (Fig. 4). The data available at present, however, suggest that the new chromosomal evidence may be a substantial help in future phylogenetic and taxonomic studies. As regards the higher level phylogeny of the parasitic Hymenoptera, new karyological evidence is especially needed for various groups of Proctotrupoidea *sensu lato* and of Chalcidoidea, especially of such apparently underived taxa as the Mymaridae, Tetracampidae and Rotoiti-

dae (Noyes 1990) and the pteromalid subfamily Cleonyminae (Boucek personal communication).

Recent investigations (e.g. Gokhman 1991b, 1994, Costa *et al.* 1993, Odierna *et al.* 1993) also show that other karyological data, especially those obtained using differential chromosome staining (e.g. C-banding), can still provide useful information even in the absence of differences in chromosome number. More detailed morphological investigations are therefore particularly likely to be of use in future species level work.

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APPENDIX I. METHODOLOGY FOR STAINING CHROMOSOMES IN ADULT PARASITIC WASPS

General comments. Chromosomes can be stained in many adult parasitic wasp females especially in recently eclosed individuals using ovarian tissue. As always in insects, care should be taken to count multiple cells so that the occasional polyploid cell can be recognised and discounted. In common with Crozier (1975) we recommend counting at least ten individual metaphase plates though occasionally this may not be possible. If fewer plates are available, one may gain extra confidence in the results if it is possible to identify through size and morphology, particular pairs of chromosomes (see for example, Fig. 9). Usually, mitotic divisions are most evident, but in some individuals and taxa, meiosis may also be observed, sometimes with very clear spreads. The number of plates may also be increased if the wasp is fed on honey water containing colchicine for a few hours before preparation, though beyond about 5 hours one stands the risk of increasing the proportion of polyploid cells. The general method described below is modified after that of Imai *et al.* (1988).

Method. Metasomas of adult female wasps are dissected in hypotonic sodium citrate solution with colchicine (Solution A). Ovaries are incubated in this solution at room temperature (c. 25°C) for 20 minutes (optimal times for different taxa may vary slightly). Following incubation, ovaries are transferred to a thoroughly cleaned microscope slide, excess citrate solution pipetted off and the slide is gently flushed with Fixative I taking care not to wash off the ovaries. Whilst still moist with Fixative I, the ovaries are disrupted (e.g. using fine mounted needles) and their cells spread gently over the middle part of the slide. One or two drops of Fixative II are then applied to the centre of the area of spread cells and the more aqueous phase which is displaced to the edge of the slide is blotted off. The same pro-

cedure is then performed with Fixative III. The slide is then air dried before staining for at least 20 minutes. Excess stain should be washed off with distilled water and the slide examined dry or under emersion oil (do not apply mounting media). Slides can be restained if the initial result was insufficiently intense, or they can be destained with alcohol in the reverse situation.

Solutions

- (A) Hypotonic sodium citrate with colchicine
1g Na citrate.2H₂O

- 5mg colchicine
100 ml distilled water
- (B) Fixative I
3 parts Ethanol
3 parts Glacial acetic acid
4 parts distilled water
- (C) Fixative II
1 part Ethanol
1 part Glacial acetic acid
- (C) Fixative III
Glacial acetic acid
- (D) Stain
2 ml Giemsa solution
50 ml 0.089M Na₂HPO₄
50 ml 0.066M KH₂PO₄

***Euryischomyia* Girault (Hymenoptera: Chalcidoidea: Aphelinidae: Eriaporinae: Euryischiini)**

MARY CARVER

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Abstract.—Types of some Australian Euryischiini described by A. A. Girault have been examined, and compared with other material identified by Girault, together with other reared and collected material of *Euryischomyia* Girault. *Euryischomyia saintpierrei* Girault, 1915, syn. nov.; *Myiocnema marmorativentris* Girault, 1915, syn. nov.; *E. fasciata* Girault, 1916, syn. nov.; and *E. setosa* Girault, 1929, syn. nov.; are placed in synonymy with *E. flavithorax* Girault & Dodd, 1915; and *E. alami* Shafee, 1975, syn. nov., (described from India), is placed in synonymy with *E. washingtoni* Girault, 1914. A key to the 2 remaining species of *Euryischomyia* is provided. *E. washingtoni* and *E. flavithorax* are redescribed. *E. washingtoni* is known as a parasite of pseudococcids, and *E. flavithorax* as a hyperparasite of psyllids, aphids, coccids and pseudococcids.

INTRODUCTION

The placement, status and composition of the subfamily Eriaporinae (Chalcidoidea: Aphelinidae) have long been a matter of uncertainty. The subfamily was erected in the family Aphelinidae by Ghesquière (1955). Members have been variously placed in the Aphelinidae (e.g. Ashmead 1900; Compere 1947; Ferrière 1965) and Elasmidae (e.g. Girault 1914; Smith and Compere 1928; Nikol'skaya 1963). Currently, the Eriaporinae are included in the Aphelinidae (e.g. Hayat 1994), albeit with some reservation (Goulet and Huber 1993). Contained taxa of Eriaporinae possess an unbroken, posteriorly expanded parastigma in the fore wing, which is usually continued posterobasally and bears 1–3 coarse, bristle-like setae.

Hayat and Verma (1980) created 2 tribes within the Eriaporinae, namely, the Eriaporini to contain the genera *Promuscidea* Girault and *Eunotiscus* Compere; and the Euryischini (*sic*) for 4 genera: *Euryischia* Riley, 1889; *Myiocnema* Ashmead, 1900; *Euryischomyia* Girault, 1914; and *Paramyiocnema* Girault, 1917. Euryischiini are characterised by possession of enlarged,

compressed hind coxae, large, bristle-like setae on the legs and elsewhere, postaxillae, a wide scutellum and a large propodeum.

The nomenclatural history of the Euryischiini is complicated by the fact that Shafee (1974) had earlier erected the family Euryischidae (*sic*) to contain *Euryischia* and, subsequently, he included *Myiocnema* and *Euryischomyia* in the family also (Shafee 1975) but, later, Shafee and Rizvi (1990) retained only *Euryischia* in the family, transferring the other 2 genera to the Aphelinidae. The elevation of these genera to family status, and their separation, are not accepted herein.

Although *Euryischia* is well characterised, the limits of the other genera of Euryischiini have not been understood and their history is also confusing. Essentially, Girault (1914) described the new genus and species *Euryischomyia washingtoni* and, in 1917, erected the genus *Paramyiocnema* for *Myiocnema marmorativentris* Girault but did not describe or diagnose the genus. Girault (1930) placed *Euryischomyia* in synonymy with *Myiocnema*. Hayat and Verma (1980) transferred *Euryischomyia flavithorax*

Girault & Dodd to *Paramyiocnema*. They also opined that *E. saintpierrei* Girault, *E. fasciata* Girault and *E. setosa* Girault might also belong in *Paramyiocnema*. Shafee *et al.* (1985) placed *Paramyiocnema* in synonymy with *Myiocnema* and Hayat (1994) placed it in synonymy with *Euryischomyia*.

The types of *Euryischomyia washingtoni*, *E. flavithorax*, *E. saintpierrei*, *Myiocnema marmorativentris*, *E. fasciata*, and *E. setosa* have been examined by the author, together with other material identified by Girault, and more recently reared and collected material of *Euryischomyia*. As a result, *Euryischomyia saintpierrei*, *Myiocnema marmorativentris*, *E. fasciata*, and *E. setosa* are placed in synonymy with *E. flavithorax*.

In addition, *E. alami* Shafee, 1975, described from India, is proposed as a junior synonym of *E. washingtoni*, thus reducing *Euryischomyia* to 2 species, namely, *E. washingtoni* and *E. flavithorax*.

METHODS

All museum material was examined as provided, as dry-mounts, or as uncleared or cleared slide-mounts. Girault's material was recognizable from information provided by Dahms (1984, 1986), and by recognition of Girault's or Mrs E.J. Girault's handwriting on the labels.

Whenever feasible, reared material was obtained by caging live, field-collected material to allow maximal mummification of already-parasitized hosts. Aphid mummies (mummified, parchment-like, sometimes silk-lined, aphid skins containing immature parasites) were removed and placed individually in gelatin capsules. Except when slide-mounted, each emergent parasite was preserved in association with its mummy. Reared material was dry-mounted, or preserved in 80% ethanol, or cleared and slide-mounted using 10% potassium hydroxide, chloral-phenol, and gum-chloral mounting media.

Micrometer eyepieces were used for measurements, all of which are of maximal values; those of the scape do not in-

clude the radicle; those of the metasoma include the ovipositor. Length of mesosoma + metasoma is given rather than body length because the head of most of Girault's specimens is separated from the trunk and slide-mounted fronto-occipitally and, in those instances of two or more mountings per coverslip, head and trunk could not be matched with confidence.

Girault customarily enumerated the number of specimens he used in a description of a new species, and then implicitly designated only 1 or 2 types from that material. Dahms (1983) considered as types all specimens stated by Girault to have been used by him in a description. Dahms' practice is followed herein.

Dahms (1984, 1986) and Hayat and Verma (1980) catalogued Girault's material of *Euryischomyia* in detail, obviating the necessity to do so herein. The information contained in the lists of specimens examined has therefore been simplified. Where appropriate, label data are enclosed in quotation marks; added or interpreted information is enclosed in square brackets. Latitudes and longitudes have in most cases been provided by the author.

The terminology adopted is that of Naumann (1991), except for the following: Antennal formula: representation of the number of segments comprising, respectively, the scape, pedicel, anellus, funiculus, club. Postaxilla: a small triangular sclerite posterior to, and apparently a division of, the mesonotal axilla; a term proposed by Shafee (1975). Parastigmal spur: a posterobasally orientated extension of the parastigmal vein, bearing 1–3 stout, bristles.

Abbreviations used include the following: ANIC, Australian National Insect Collection, Canberra; BMNH, British Museum (Natural History), London; QM, Queensland Museum, Brisbane; SAM, South Australian Museum, Adelaide; USNM, United States National Museum of Natural History, Washington DC; WADA, Western Australian Department of Agriculture,

South Perth; ZMA, Zoological Museum, Aligarh.

Euryischomyia Girault

Euryischomyia Girault, 1914: 285.—Girault 1915a: 178; Girault 1930: 1; Shafee 1975: 27; Hayat & Verma 1980: 35; Hayat 1983: 87; Dahms 1986: 689; Viggiani 1988: 101; Shafee & Rizvi 1990: 103.

Euryischomyia [sic] Girault, 1929: 331.

Paramyiochisma Girault, 1917: 93.—Hayat 1994: 85.

Type species *Euryischomyia washingtoni* Girault, by monotypy and original designation.

The following characters, in combination, are diagnostic for *Euryischomyia*:

Head with 7 pairs of long, stiff setae near ocelli and inner orbital margins; maxillary and labial palps 2-segmented; mandibles tridentate (or, depending on interpretation, bidentate, the wide dorsal tooth being apically concave and truncate); setose. Antennae: scape unexpanded in both sexes; 1–2 anelli; funicle 3-segmented; club 3-segmented.

Pronotum with row of long, stiff setae, 3 on each side, posterosublaterally. Mesoscutum between notauli with 2–3 rows of shorter, finer setae anterior to row of 4 and row of 2 longer, stiffer setae; scutellum wider than long, with 2 pairs of long, stout setae, otherwise bare. Postaxillae present, bare. Phragma evenly tapered, apically incised. Metanotum not produced posteromedially. Propodeum wide, not excavated posterolaterally.

Fore wings hyaline or medially infuscated; parastigmal spur little- or well-developed, with 1–2, rarely 3, long, bristle-like setae of similar size to those on submarginal vein; 0–2 bristle-like setae posterobasal to parastigma, or area posterior to submarginal vein and proximal of parastigmal spur with 6–13 shorter, stiff setae in 2–3 irregular rows; this area of disc otherwise bare; discal setation proximally regularly or irregularly margined.

Legs: hind coxa enlarged, elongate-ovate, bilaterally compressed ventrally; hind femur elongate, broad, laterally compressed, laminose and arcuate in section; fore and mid femora also broad and laterally compressed. Only one hind tibial spur. Long, bristle-like setae on legs most commonly disposed in differently sized pairs (as subapically on coxae) or in longitudinal rows (as on mid and hind tibiae).

Petiole wide, boomerang-shaped. Bases of cerci low, tuberculate.

Notes.—*Euryischomyia* is most closely related to (the monotypic) *Myiocnema*, which differs in possessing 2 hind tibial spurs, 3-segmented maxillary palps, 3 anelli, and a distinctive fore wing chaetotaxy; the costal cell bears numerous short, stiff setae, and the basal discal area bears both a very long bristle-like seta posterior to the parastigmal spur and several irregular rows of shorter, stiff setae in the angle between the submarginal vein and the parastigmal spur. The chaetotactic differences may be of specific value only. Studies in progress by J.B. Woolley and M. Hayat show that *Myiocnema* differs significantly from *Euryischomyia* in not possessing a looped mesofurca (Hayat 1994).

Euryischia is very distinctive in possessing almost circular, disc-like hind coxae, a posterolaterally excavated propodeum to accommodate the coxae, and a postero-medial metanotal process ('elasmid' characteristics). *Euryischia* is further distinguishable from *Euryischomyia* in possessing 2 hind tibial spurs, 4-segmented maxillary palps, and cylindrical cercal bases. The scape of the male of some species of *Euryischia* is greatly enlarged, and the chaetotaxy of the mesonotum and fore wing of *Euryischia* is interspecifically variable. Hayat and Verma (1980) provided keys to the genera.

Taxa of Euryischiini clearly demonstrate different degrees of development of eriporine and euryischiine features, namely, development of the parastigmal spur; spi-

nosity of the legs, fore wing and body; enlargement and compression of the hind legs and concomitant modifications of the mesosoma. *Euryischia washingtoni*, *E. flavi-*

thorax, *Myiocnema comperei* Ashmead and *Euryischia* spp. are successively more endowed in these respects.

KEY TO SPECIES OF *EURYISCHOMYIA* GIRAULT

1. Parastigmal spur well-developed, bearing 2, rarely 3, long, bristle-like setae. Area immediately posterior to submarginal vein and proximal to parastigmal spur with 2–3 irregular rows of 6–13 relatively small, stiff setae. Subapical margin of costal cell with 4–7 short, stiff setae anterior to cluster of fine, ventral setae; otherwise bare. Fore wings hyaline, not narrow. Mesoscutum with 11–21 setae in 2–3 irregular rows anterior to row of 4 and row of 2 bristle-like setae. Body coloration yellow, orange, brown and black. Distribution: Australia. *E. flavithorax* Girault
- Parastigmal spur scarcely developed, bearing 1–2 bristle-like setae. Area posterobasal to parastigma bearing 0–2 large, bristle-like setae. Costal cell ventro-subapically with some pale, fine setae; otherwise bare. Forewings narrow, 3.5 times longer than width; medially with broad band of infuscation. Mesoscutum with only 8 setae anterior to row of 4 and row of 2 setae. Body coloration predominantly black, legs predominantly lemon-yellow. Distribution: Australia and India. *E. washingtoni* Girault

Euryischomyia washingtoni Girault

Euryischomyia washingtoni Girault, 1914: 285.—Girault 1915a: 178; Hayat & Verma 1980: 37; Dahms 1986: 649.

Euryischomyia alami Shafee, 1975: 27.—Hayat & Verma 1980: 37. **Syn. nov.**

Type Material Examined.—*Euryischomyia washingtoni* Girault: Lectotype ♀, paralectotype ♂ (both on 1 slide, also parts of holotype of *Pleurotropomyia seditiosus* Girault; all separate); paralectotype ♀, (on tag, minus head). (QM 4060; [Hy]2742). QUEENSLAND: 20°32'S 145°24'E Capeville (Pentland), by sweeping in forest along the banks of Cape River, 8.i.1913 (Girault 1914).

Other Specimen Examined; Identified by A.A. Girault.—"Euryischomyia [sic] washingtoni" ♀ (on tag and on slide; slide also contains a paratype of *Anicromelus grandaeus* Girault). QUEENSLAND: 17°23'S 145°19'E Watsonville (QM).

Other Records.—*Euryischomyia washingtoni*: QUEENSLAND: 19°15'S 146°48'E Townsville, sweeping in forest, 19.i.1913, ♀ (Girault 1915a).

Euryischomyia alami: ex *Nipaecoccus viridis* (Newstead) on *Mangifera indica*, MY-SORE: Bangalore, Channapatna, 2.xii.1968, holotype ♀, paratype ♀, S.A. Shafee (Shafee 1975) (ZMA).

Euryischomyia alami: ex *Nipaecoccus viridis*, TAMIL NADU: Shencottah, 2♀♀, M. Hayat (Hayat and Verma 1980) (ZMA).

Redescription.—Coloration of ♀: Body shiny, blackish brown to black; mesonotum obscurely dark green metallic. Body setae mostly pale. Legs whitish except for following: fore coxae dusky basally; mid and hind coxae black except apically; mid and hind femora black except apically and basally; tarsi brown apically; sockets of hind tibial bristles black. Fore wings each with broad band of pale to dark infuscation extending from anterior to posterior margins in region of marginal and post-marginal veins, otherwise hyaline.

Morphology: Length mesosoma + metasoma: 0.90 mm (paralectotype ♀); 1.05 mm (lectotype ♀); 1.40 mm (♀ ex Watsonville); 0.84 mm (paralectotype ♂). All bristle-like setae smaller and finer than corresponding ones of *E. flavithorax*.

Head: submedian frontal setae (of ♂): (48 μm); interocellar setae: (68) μm. Maxillary and labial palps longer and more slender than in *E. flavithorax*. Dorsalmost tooth of mandibles pointed.

Antennae of ♀ *ex* Watsonville (and ♂): antennal formula: 1:1:1-2:3:3; relatively longer and more slender than in *E. flavithorax*. Scape: length 5.56 (4.44) × maximal width; 1.82 (1.73) × length of pedicel; 1.22 (1.11) × length of club. Pedicel: 2.5 (2.28) × maximal width. Anellus small, wedge-shaped; a 2nd anellus may be partly delimited from it. Funicular segments mostly as long as or longer than wide; segment 1 (f1): length, 1.18 (1.0) × width; f2: length, 1.41 (0.94) × width; f3: length 1.04 (1.14) × width. Club: length: 2.56 (3.56) × width. Lengths of segments: scape, 150 (107) μm; pedicel, 83 (62) μm; f1: 30 (20) μm; f2: 47 (21) μm; f3: 41 (30) μm; club: 123 (96) μm.

Mesosoma of lectotype ♀ (and ♂): Pronotum: 6 bristle-like setae postero-sublaterally, 68 (75) μm long. Mesoscutum between notauli with row of 2, and row of 6, fine, bristle-like setae, 33 (26-29) μm long; row of 4 (38) μm long; and row of 2 thicker, bristle-like setae (51) μm long. 2 midsublateral and 2 posterolateral scutellar setae, (45 μm) and 90 (93) μm long, respectively. Axilla with 2 setae; posterior seta (34) μm long.

Legs of lectotype ♀ (and ♂): Hind coxa, 0.21 (0.22) mm long, 1.87 (1.74) × width, slightly shorter than hind femur, which is shorter than hind tibia; subapical setae of hind coxa: 30 (36) and 48 (54) μm long; hind femur, 0.23 (0.26) mm long, 2.53 (2.74) × width, subapical seta, 26 (30) μm; hind tibia, 0.31 mm long, gradually broadening apicad, preaxial row of setae maximally 50 μm long, subapical setae 44 and 62 μm long, spur 48 μm long.

Fore wings of lectotype ♀ (and ♂) narrow, 3.5 × width. Parastigmal spur hardly developed, bearing 1-2 bristle-like setae, 45 μm long; 1 or 2 bristle-like setae posterobasal of parastigma, 31 (35) μm and (18) μm long, respectively. Subapical area

of costal cell devoid of marginal setae. Discal setation with regular margin.

Metasoma in dry-mounted ♀♀ upturned at an angle of approximately 60°, strongly tapered apicad.

Ovipositor sheaths 0.18 mm long, 0.59 × hind tibial length, slightly protrusive beyond apex of metasoma, densely and evenly furnished with short, bristle-like setae.

Notes.—Based on a knowledge of the chaetotactic variability within the tribe, *E. alami* is hereby placed in synonymy with *E. washingtoni*, despite the fact that the types of *E. alami* have not been seen by the present author. *E. alami* reportedly differs from *E. washingtoni* in not bearing discal setae posterior to the parastigma, and in possessing 3 setae anteriorly on the axilla (Shafee 1975; Hayat and Verma 1980). These differences are too small to warrant separation at the species level. Hayat and Verma (1980), who studied the above-listed specimens from Tamil Nadu, are also of the opinion that the differences between the 2 taxa appear to be of doubtful specific value.

The above description of *E. washingtoni* supplements those of Girault (1914, 1915a) and Hayat and Verma (1980) of *E. washingtoni* and that of Shafee (1975) of *E. alami*. Because of the paucity and poor condition of the material available for study, a composite and comparative method of description is adopted. *E. flavithorax*, the standard of comparison, is conventionally described below in greater detail. The lemon yellow coloration described by Girault (1914, 1915a) can be presumed to have faded with time to white. The antenna of the paralectotype ♀ (on slide) is compressed; measurements and ratios of the ♀ *ex* Watsonville are given instead.

E. washingtoni has less developed euryischiine features than the other taxa of Euryischiini, having a scarcely developed parastigmal spur, and shorter, finer bristle-like setae on the body, limbs and fore wings.



Fig. 1. *Euryischomyia flavithorax*, male ($\times 67$). Cleared, slide-mounted specimen.

Biology.—Parasite of unknown status of *Nipaecoccus viridis*, Pseudococcidae.

Distribution.—AUSTRALIA: Queensland; possibly also Beenleigh, Victoria (Viggiani 1988); INDIA: Mysore, Tamil Nadu.

Euryischomyia flavithorax

Girault & Dodd

(Figure 1)

Euryischomyia flavithorax Girault & Dodd, 1915 in Girault 1915a: 178.—Dahms 1984: 614.

Euryischomyia saintpierrei Girault, 1915a: 178.—Hayat & Verma 1980: 37; Dahms 1986: 495.

Syn. nov.

Myiocnema marmorativentris Girault, 1915b: 64.—Dahms 1984: 795. **Syn. nov.**

Euryischomyia fasciata Girault, 1916: 212.—Hayat & Verma 1980: 37; Dahms 1984: 579. **Syn. nov.**

Paramyiocnema marmorativentris (Girault).—Girault 1917: 93; Hayat & Verma 1980: 35.

Euryischomyia setosa Girault, 1929: 331.—Hayat & Verma 1980: 37; Dahms 1986: 522. **Syn. nov.**

Paramyiocnema flavithorax (Girault & Dodd).—Hayat & Verma 1980: 33.

Type Material Examined.—*Euryischomyia flavithorax* Girault & Dodd: Lectotype ♀ (on slide); paralectotype ♀ (on tag; head and hind tibia on same slide as lectotype, herein called paralectotype 1); paralectotype ♀ (also on same slide as lectotype, herein called paralectotype 2). QUEENSLAND: 17°05'S 145°47'E "Gordonvale (Cairns)" (QM 3903; Hy2744).

Euryischomyia saintpierrei Girault: Holotype ♀ (torso and 1 fore wing on tag, fore wing separate, not listed by Dahms (1986); head, funicular segments 2 and 3 and club, both hind legs on slide) (QM 3905; Hy2743). QUEENSLAND: 27°28'S 153°02'E Brisbane (Girault 1915a).

Myiocnema marmorativentris Girault: Holotype ♀ (on slide) QUEENSLAND: 17°05'S 145°47'E "Gordonvale (Cairns)" (QM 3907; Hy2959).

Euryischomyia fasciata Girault: Holotype

♂ (not ♀, as described by Girault; on tag minus antennae, right wings and leg parts; antenna minus scape, fore wing, hind femur and hind tibia on slide; antenna not listed by Dahms (1984)). WESTERN AUSTRALIA: 31°57'S 115°51'E "Perth, W. Austr., G. Compere, Collector, 837" (USNM 19679).

Euryischomyia [sic] *setosa* Girault: Holotype ♀ (on tag, minus head, with 1 fore wing on slide) SOUTH AUSTRALIA: 32°49'S 138°11'E "Melrose, Oct., A.M. Lea" (SAM).

Other Specimens Examined: identified, as follows, by A.A. Girault.—"Myiocnema flavithorax Gir. [sic], brown scale [*Coccus hesperidum*] parasites, [WESTERN AUSTRALIA:] ♀, [2]♂♂, coll. L.J. Newman, 70". (On 1 slide. Host identified as *Coccus hesperidum* in F. Wilson (1960)). (WADA).

Euryischomyia [sic] *flavithorax* Gir. [sic], ♀. Host Lecanidae [Coccidae] sp. Ent. Div. Dep. Ag. & Stk Qld." (QM Hy 10).

"*Myiocnema saintpierrei* Gir., ♂, ♀. Host *Saissetia* sp., Sydney [33°53'S 151°12'E], N.S.W., June 19–31, S.E. Flanders. Univ. Cal. Citrus Exp. Sta. Acc. No. 27)." (On slide; only 2 of 6 specimens easily observable). (QM).

"*Myiocnema setosa* Gir., ♀, *Myiocnema saintpierrei* Gir., ♂, ♀, on lime scale [Coccidae?], [QUEENSLAND: 26°45'S 150°38'E] Chinchilla, Aug. 14, 1931, S.E. Flanders". (On slide; only 2♀♀, 2♂♂ easily observable) (QM).

Other Specimens Examined.—QUEENSLAND: 15°39'S 144°31'E Split Rock, 28.v.–26.vi.1993, ♀, P. Zborowski, I.D. Naumann (ANIC).

WESTERN AUSTRALIA: 33°45'S 122°32'E Condingup, 55km E of Esperance, 30.xii.1986, ♂, J.S. Noyes (BMNH).

ex *Psyllaephagus* sp. / *Cardiaspina albitextura* Taylor on *Eucalyptus blakelyi*, VICTORIA: nr 36°21'S 146°19'E Wangaratta, 11.ii.1955, 3♀♀, 7♂♂, E. Lewis (ANIC).

ex *Cardiaspina* sp. on *Eucalyptus blakelyi*, AUSTRALIAN CAPITAL TERRITORY: 35°18'S 149°08'E Canberra (site 15a),

3.ii.1954, 2♀♀, A. Magassy. NEW SOUTH WALES: 35°50'S 147°15'E Woomargana, 3.xii.1954, ♀, E. Lewis (all in ANIC).

ex *Creiis* sp., WESTERN AUSTRALIA: 31°59'S 115°52'E Western Australian Institute of Technology, South Perth, 1982, ♀, S.J. Curry (ANIC).

ex *Aphidius colemani* Viereck / *Brachycaudus helichrysi* (Kaltenbach) on safflower, NEW SOUTH WALES: 29°14'S 149°51'E 25km N. of Moree, 12.ix.1993, 3♀♀, 1♂, J. Stanley (ANIC).

ex *Aphidius colemani* / *Myzus persicae* (Sulzer) on nectarine, AUSTRALIAN CAPITAL TERRITORY: 35°15'S 149°05'E Aranda, Canberra, 15.xi.1991, 2♀♀, P.J. Hart (ANIC).

ex *Trioxys complanatus* Quilis / *Therioaphis trifolii* (Monell) f. *maculata* on lucerne, VICTORIA: 36°25'S 145°56'E Goorambat, 1979, ♀, P. Ridland; 36°33'S 145°59'E Benalla, 9.ii.1978, ♀, 2♂♂, L.T. Woolcock; SOUTH AUSTRALIA: 34°40'S 138°34'E Virginia, 21.ii.1980, ♂, C. Wilson; 34°56'S 138°36'E Northfield, Adelaide, 20.iii.1978, 8.ii.1979, 4♀♀, 3♂♂, L.T. Woolcock; 35°41'S 139°20'E Meningie, 27.ii.1979, ♂, C. Wilson (all in ANIC).

ex *Aphelinus mali* (Haldeman) / *Eriosoma lanigerum* (Hausmann) on apple, NEW SOUTH WALES: 30°31'S 151°40'E Armidale, December 1992, 6♀♀, S. Asante (ANIC).

ex *Pseudococcus* sp., on *Acacia melanoxylon*, VICTORIA: 37°42'S 145°04'E LaTrobe University, Bundoora, Melbourne, 1.xii.1980, 2♀♀, 2♂♂, G. Farrell (BMNH).

Other records.—QUEENSLAND: 15°28'S 145°15'E Cooktown, in forest, 2.iii.1914, ♀, A.P. Dodd (Girault 1915a; Dahms 1984).

WESTERN AUSTRALIA: 27°41'S 114°33'E Kalbarri National Park, December 1986, ♀, J.S. Noyes; 31°36'S 116°13'E Avon Valley National Park, 50km NE of Perth, 25.xii.1986, ♀, J.S. Noyes; 31°43'S 116°04'E Walyunga National Park, 40km NE of Perth, 24.xii.1986, ♂, J.S. Noyes (BMNH) (Identified by L.D. Coote).

ex *Ceroplastes rubens* Maskell on *Scheff-*

flera actinophylla, QUEENSLAND: 27°30'S 153°01'E Brisbane, May 1980, 4♂♂, J.S. Noyes (BMNH) (Recorded as *Paramyioec-nema* sp. by Viggiani (1988)).

Redescription of Female.—Coloration: Most body setae dark. Head yellow, orange or tawny except for following: brown, linear macula suborbitally on gena; small, brown macula surrounding posterior half of median ocellus and anterior half of each lateral ocellus; extensive, broad, brown to black, inverted U-shaped macula in region adjacent to prothorax; mandibles apically testaceous. Antennae yellow, scape may be dusky. Eyes red; margin and, internally, medial half of eye socket darkly sclerotized (conspicuous only in cleared specimens). Ocelli red.

Mesosoma, orange or tawny except for following dark sclerotization: extensive, brown to black macula on prothorax adjacent to occipital region of head; notauli anteriorly, boundaries of anterior angles of axillae, anterior and posterior boundaries of pronotum, scutellum and metanotum may be brown; 1–2 small, brown to black maculae near base of fore wing; sometimes 1 macula at base of posterolateral setae of scutellum and submarginally on metanotum; propodeum light to dark brown anteriorly and on each lateral third except for spiracles, lateral margins may be darker, or whole segment may be brown and laterally black. Ventrally and sometimes pleurally, mesosoma light brown to dark brown.

Legs yellow except for following: fore femur with linear macula postaxially; mid coxa may be slightly dusky basally; hind coxa brown to dark brown except usually apically, sometimes also dark brown marginally; hind femur sometimes streakily dusky; sockets of hind tibial bristles black.

Metasoma light brown to black; petiole usually brown, often black on lateral margins; base of gaster medially and gastral tergites 2–4 usually darker than rest of gaster, and fasciate, especially under high magnification.

Morphology: Length mesosoma + metasoma, 0.7–1.3 mm long (mean, 1.01 mm; $n=20$; lectotype, 1.06 mm). Integument variously reticulate-imbricate, except that of most of metanotum and propodeum, which is smooth; imbrication on tibiae finely setose at interstices. Large setae longitudinally ridged.

Head: 2 pairs of large, stiff, bristle-like setae on frons near margins of eyes; 1 submedian pair between these (100 μ m long in lectotype); 1 pair lateral to median ocellus; 1 pair near margin of eyes anterolateral to lateral ocelli; 1 pair between lateral ocelli (113 μ m); 1 pair posteromedial to lateral ocelli. Dorsalmost tooth of mandible usually slightly blunt.

Antennae inserted not far distant from clypeal margin, the distance subequal to distance between insertions; setae short, with stouter, stiffer hairs concentrated on one side; antennal formula: 1:1:1–2:3:3. Scape: length, 2.9–3.4 \times width (mean, 3.2); 1.7–2.3 (2) \times length of pedicel; 1–1.2 (1.1) \times length of club. Pedicel: length, 1.3–2.5 (1.8) \times width; 0.6–1 (0.75) \times length of anellus(i) + funicle. Anellus 1 large enough to be considered funicular, finely setose but non-sensoriated; a 2nd, very small, anellus sometimes variously developed on half of apex of anellus 1, may be setose. Funicular segments all wider than long, becoming progressively wider and longer apicad; segment 1 (f1) length, 0.58–0.87 (0.7) \times width; f2: length, 0.47–0.82 (0.74) \times width; f3: length, 0.64–0.9 (0.79) \times width; length of anellus (i) + funicle, 0.6–0.9 (0.7) \times club. Club 3-segmented; segments separable by segmentally arranged setal and sensorial patterns, not by sutures; length, 1.5–2.7 (2) \times width; width 1–1.8 \times width of f3. Lengths of segments: scape, 99–135 μ m (mean, 117 μ m; $n=20$); pedicel, 45–68 (58) μ m; f1, 14–24 (17.5) μ m; f2, 12–37 (24) μ m; f3, 24–41 (31) μ m; club, 93–123 (107) μ m.

Mesosoma: Pronotum with row of 3+3 long setae (115 μ m long in lectotype) posterosublaterally. Mesoscutum anteriorly,

between notauli, with 11–21 fine, stiff setae ($41\text{ }\mu\text{m}$) in 2–3 irregular rows; a middle transverse row of 4 long, stout setae ($98\text{ }\mu\text{m}$), and posterior row of 2 long, stout setae ($90\text{ }\mu\text{m}$). Scutellum with 2 long setae anterosublateral of midpoint ($87\text{ }\mu\text{m}$) and 2 very long, stout setae posterolaterally ($168\text{ }\mu\text{m}$). Axillae each with long, stout seta ($84\text{ }\mu\text{m}$) anteriorly and 2–3, rarely 4, shorter, differently sized setae ($26\text{--}36\text{ }\mu\text{m}$) near posterior angle. Mesosomal setae of smaller specimens shorter and less stout.

Legs bearing long, stiff setae, mostly in rows or in differently sized pairs; other setae mostly disposed dorsoapically on femur and longitudinally on tibia; Fore coxa (of 1 Northfield specimen): pair of long, stiff setae subapically (39 and $57\text{ }\mu\text{m}$ long); fore femur: subapically, 1 seta ventrally ($29\text{ }\mu\text{m}$), 1 dorsally ($45\text{ }\mu\text{m}$); fore tibia appearing fusiform, calcar plumose ($57\text{ }\mu\text{m}$), 3 small, stiff setae apically ($31\text{ }\mu\text{m}$), and row of 7 setae (maximally $31\text{ }\mu\text{m}$) preaxially. Mid coxa: pair of setae subapically (42 and $57\text{ }\mu\text{m}$); mid femur: very long pair subapically ($65\text{ }\mu\text{m}$ ventrally, $78\text{ }\mu\text{m}$ dorsally); mid tibia: spur long ($87\text{ }\mu\text{m}$), plumose, 1 smaller seta near spur ($18\text{ }\mu\text{m}$), 1 subapically ($53\text{ }\mu\text{m}$), preaxial row (maximally $32\text{ }\mu\text{m}$) hardly differentiated from other setal rows. Hind coxa (0.22 mm long), shorter than hind femur (0.28 mm), which is slightly shorter than hind tibia (0.32 mm) and subequal to hind tarsus (0.27 mm); hind coxa large, elongate-ovate, length $1.44\text{--}1.69 \times$ width, bilaterally compressed ventrally, pair of setae subapically (44 and $66\text{ }\mu\text{m}$); hind femur broad, approximately parallel-sided, length $2.83\text{--}3.14 \times$ width, 1 seta subapically ($58\text{ }\mu\text{m}$); hind tibia, basally narrow, gradually and slightly widening apicad, spur almost smooth ($54\text{ }\mu\text{m}$ long), pair of very long, stout setae subapically (68 and $89\text{ }\mu\text{m}$) and 1 longitudinal row of 8 very long, stout setae (maximally $75\text{ }\mu\text{m}$). Mid basitarsus longer than fore or mid basitarsus, but not conspicuously long.

Fore wings: 6–13 (mean, 10) moderately

long and fine, stiff setae ($30\text{--}40\text{ }\mu\text{m}$ long in 1 Northfield specimen) present in 2–3 rows below submarginal vein and proximal of parastigmal spur; 2–3 parastigmal setae ($70\text{--}76\text{ }\mu\text{m}$); costal cell in distal third with 4–7 short, stiff, marginal setae ($25\text{ }\mu\text{m}$) anterior to cluster of fine, stiff, ventral setae; margin of discal setation irregular.

Metasoma not upturned or strongly tapered: Petiole boomerang-shaped except for truncated ends. Various sized, stiff setae metamERICALLY disposed laterad and apicad on dorsum of gaster.

Ovipositor sheaths $0.10\text{--}0.11\text{ mm}$ long, $0.23\text{--}0.33 \times$ hind tibial length, each furnished with about 10 mostly subapical setae.

Description of Male.—Similar to female. Colour pattern similar but yellower because of less extensive dark sclerotization. Linear macula usually present, anteromedially, on vertex; suborbital, linear macula of gena absent and U-shaped macula of occipital region absent. Mesosoma laterally pale. Gaster: dark sclerotization confined to narrow area adjacent to petiole and to medially coalesced fascia on gastral tergites 2–4, extending medially on gastral tergite 5 and apicolaterad.

Antennae (1 specimen): scape: length, $111\text{ }\mu\text{m}$, $3.7 \times$ width, $2.18 \times$ length of pedicel, $1.19 \times$ length of club; pedicel: length, $51\text{ }\mu\text{m}$, $1.7 \times$ width, $0.71 \times$ length of anellus + funicle; funicular segment 1 (f1): length, $12\text{ }\mu\text{m}$, $0.47 \times$ width; f2: length, $21\text{ }\mu\text{m}$, $0.66 \times$ width; f3: length, $27\text{ }\mu\text{m}$, $0.66 \times$ width; anellus + funicle: length, $0.77 \times$ length of club; club: length, $0.93\text{ }\mu\text{m}$, $1.32 \times$ width.

Hind coxa 0.24 mm long, twice as long as wide; hind femur 0.24 mm long, $3.2 \times$ width; hind tibia 0.3 mm long.

Mesosoma + metasoma 0.9 mm long. Anterior mesoscutal setae, $33\text{--}45\text{ }\mu\text{m}$ long; mid and posterior setae, 70 and $81\text{ }\mu\text{m}$ long respectively. Anterior and posterior scutellar setae 64 and $121\text{ }\mu\text{m}$, respectively; only 1 posterior axillar seta, $24\text{ }\mu\text{m}$ long.

Notes.—The type material of *E. flavithor-*

ax comprises the slide-mounted lectotype designated by Hayat in 1979 (Hayat and Verma 1980), and paralectotype 1, with parts on a tag and parts on the same slide as the lectotype but mounted separately, inbetween the lectotype and paralectotype 2 (see list of type material examined). Paralectotype 2 is the specimen stated by Hayat and Verma (1980) to be a species different from the lectotype, resembling *marmorativentris*, and probably not part of the original type material. Consequent upon the above statements, the specimen was referred to by Dahms (1984) as an unidentified chalcidoid. Paralectotype 2 is, without doubt, *Euryischomyia flavithorax*. Smaller and yellower than the lectotype, it does indeed resemble the holotype *Myiocnema marmorativentris*, which was collected in the same locality a week or so later.

The female collected by A.P. Dodd at Cooktown has still not been located (see list of other records above). It may be part of Dodd's collection.

E. flavithorax was originally described from 3 swept specimens, and each of the synonymized species was described from single specimens. The relevant parts of the descriptions are based mainly on coloration. Other characters described by Girault are supra-specific or are not interspecifically comparable. However, all of them fit into the above conception of *E. flavithorax*.

E. flavithorax is variable in coloration. In general, smaller females are yellower and less darkly sclerotized than larger ones, and males are smaller and yellower than females. The differences are a reflection of differences in extent of dark sclerotization. The pattern of coloration, however, is constant, and is best expressed in the lighter-coloured specimens. The lectotype of *E. flavithorax*, for instance, belongs near the large, dark end of the scale of variability, whereas paralectotype 2 of *E. flavithorax* and the holotype *M. marmorativentris* belong near the small, pale end. The small, pale holotype *E. fasciata* is a male.

Girault (1915a) described *E. saintpierrei*

as possessing 2 anelli, which may have been the reason why he considered it a species distinct from the other species of *Euryischomyia*, and why he identified specimens from 'lime scale' as 2 species, *M. saintpierrei* and *M. setosa* (see above list of specimens identified by Girault). These specimens, on 1 slide, have antennae each with either 1 or 2 anelli but are otherwise similar to one another. Most of the specimens of *E. flavithorax* examined in this study have both antennae with 1 anellus; others have 2; or 1 antenna may bear 1 anellus and the other bear 2; or 1 small anellus may be partly delimited from a larger one.

Distribution.—AUSTRALIA: Queensland, New South Wales, Australian Capital Territory, Victoria, South Australia, Western Australia (Figure 2).

Biology.—*E. flavithorax* is not highly host-specific, its recorded hosts being chalcidoid and ichneumonoid Hymenoptera, and psyllid, aphidoid and coccoid Hemiptera Sternorrhyncha (Table 1). *E. flavithorax* was reared occasionally from immature Aphidiinae and *Aphelinus mali*, endoparasitic in aphidine and drepanosiphine, and pemphigine aphids, respectively, as part of a long-term study by the author of aphids and their insect natural enemies; and, also occasionally, from *Psyllaephagus* sp(p). parasitic in lerp-forming psyllid nymphs, as part of an ecological study by L.R. Clark in 1950–74 of psyllids associated with eucalypts (Riek 1962).

E. flavithorax, however, is not a true hyperparasite of aphids if, like certain other chalcidoids and proctotrupoids (e.g. *Pachyneuron* spp. (Pteromalidae) and *Dendrocerus* spp. (Megaspilidae) (Takada 1973a,b)), it does not parasitize the hymenopterous host until after the latter has consumed all of its aphid host except for the dead, dry aphid skin (mummy); i.e. if it parasitizes the hymenopterous contents of a capsule it is strictly a primary parasite. Such a probability is supported by its broad host spectrum; parasitizing live hosts of such

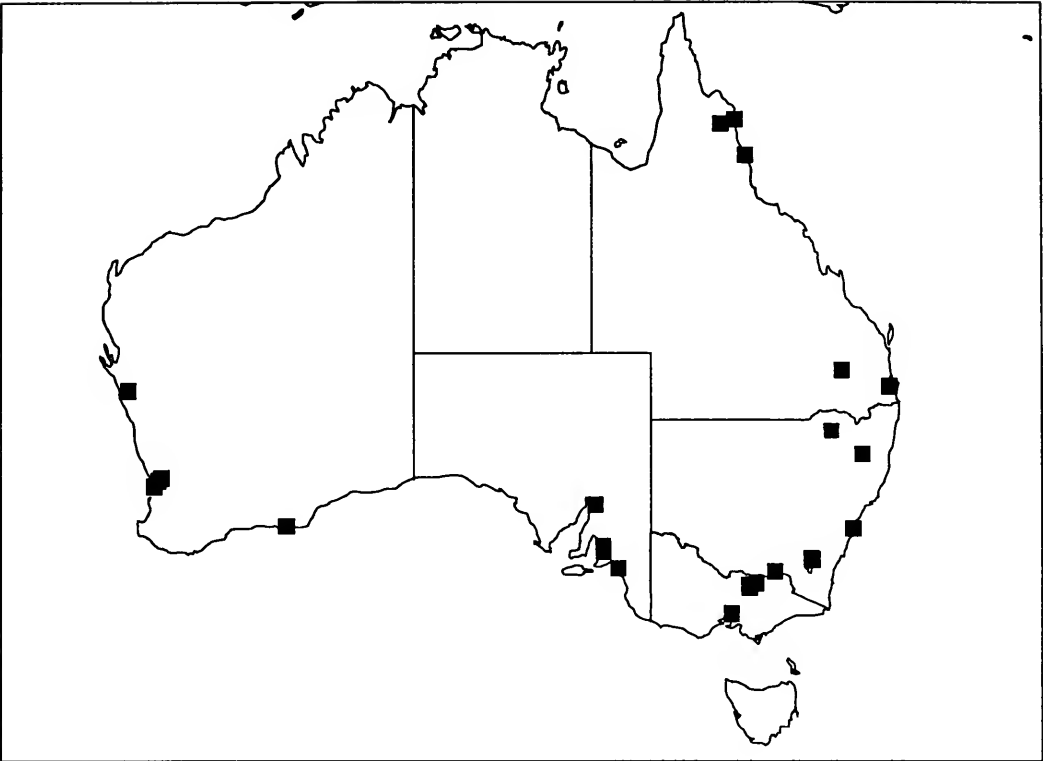


Fig. 2. Known distribution of *Euryischomyia flavithorax*.

Table 1. Hosts of *Euryischomyia flavithorax*

| Hemiptera: Sternorrhyncha | Hymenoptera |
|---|---|
| Psylloidea: Psyllidae: Spondyliaspidae: <i>Cardiaspina albitextura</i> <i>Cardiaspina</i> sp. <i>Creiis</i> sp. Aphidoidea: Aphididae: Aphidinae: <i>Brachycaudus helichrysi</i> <i>Myzus persicae</i> Drepanosiphinae: <i>Therioaphis trifolii</i> f. <i>maculata</i> Pemphiginae: <i>Eriosoma lanigerum</i> Coccoidea: Pseudococcidae: <i>Pseudococcus</i> sp. Coccoidea: Coccidae: <i>Ceroplastes rubens</i> <i>Coccus hesperidum</i> <i>Saissetia</i> sp. | Chalcidoidea: Encyrtidae: <i>Psyllaephagus</i> sp. Ichneumonoidea: Braconidae: Aphidiinae: <i>Aphidius colemani</i> <i>Aphidius colemani</i> <i>Trioxys complanatus</i> Chalcidoidea: Aphelinidae: <i>Aphelinus mali</i> |

morphological and behavioral diversity would demand a high degree of reproductive adaptability.

Its status as a parasite of Coccoidea is uncertain. Female coccids, being sessile and capsule-like, could conceivably function as either primary or secondary hosts.

E. flavithorax is exclusively Australian, as far as known. The original hosts are likely to be native sternorrhynchous Hemiptera and Hymenoptera, e.g. spondyliaspidine psyllids and their *Psyllaephagus* parasites. The recorded aphid hosts and their primary parasites, and the coccoid hosts, are all exotic species introduced into Australia.

E. flavithorax was collected throughout the year but most commonly in summer (December and February). *E. flavithorax* (recorded as *Myiocnema* sp.) comprised 2% of the emergent parasites of *Trioxys complanatus* / *Therioaphis trifolii* f. *maculata* in several sites in South Australia between 1977 and 1980 (C.G. Wilson and Swincer 1984).

Females were commoner than males, especially among collected rather than reared material.

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Male Nest Defense in the Digger Wasp *Cerceris binodis* (Hymenoptera: Sphecidae)

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Abstract.—Male *Cerceris binodis* (Hymenoptera: Sphecidae: Philanthinae) defend territories that contain nesting females from conspecific males. A female which is provisioning a nest will mate when she returns to the nest and a male is present. This mating system represents the first description of male nest defense in the genus *Cerceris*. Presumably, this behavior occurs in *C. binodis* because females nest in aggregations, and mate multiply.

INTRODUCTION

The cosmopolitan genus *Cerceris* contains over 800 species (Bohart and Menke 1972), more than any other sphecid genus, but mating systems of relatively few *Cerceris* species have been studied. Non-resource based territoriality has been reported in all *Cerceris* mating systems which have been described (Alcock 1975a, Evans 1971, Evans and O'Neill 1985, Evans and O'Neill 1988), and in four other genera in the sphecid subfamily Philanthinae: *Aphilanthops*, *Philanthus*, *Clypeadon*, and *Eucerceris* (Evans and O'Neill 1988; O'Neill 1990). In this mating system, males apply volatile secretions originating from mandibular glands to a substrate with clypeal brushes, and defend these non-resource based territories from conspecific males. Philanthine females typically nest in dispersed conditions, mate once at the beginning of the nesting period away from the nest, presumably are attracted to mandibular gland secretions, and enter territories to copulate (Evans and O'Neill 1988). The mating system of *C. binodis* departs from these conditions. Females nest in aggregations, and mate multiply at the nest. Resident *C. binodis* males stand on or directly adjacent to nests, exclude conspecific non-resident

males from nests, and do not scent mark territories. Of the eight philanthine genera, male nest defense has been described only in *Philanthus*, and presumably is derived within that genus (Evans and O'Neill 1988). Male nest defense is described here for the first time in the genus *Cerceris*, and also presumably represents a derived condition within this taxon.

METHODS

An aggregation of nesting *C. binodis* females was discovered on Barbour Lathrop trail on Barro Colorado Island, Republic of Panama on July 8, 1994. A group of five nests that were close enough together to be observed simultaneously were marked with numbered tags. Male and female wasps were individually marked with enamel paint on the thorax, and head widths were measured to the nearest 0.05 mm with Manostat calipers. The nests were observed on two days after individuals were marked. Observations were made from 1355-1525h on the first day, and from 1515-1650h on the second day. The behaviors recorded were the amount of time that males spent standing on or adjacent to nests, defensive interactions between males, and copulations.

RESULTS

When a female returned to a nest with prey, and a resident male was present, she would land on the nest tumulus, and copulate. However, a female would fly directly into her nest if no male was present. This behavior is also described in the sphecid genus *Oxybelus* (Crabroninae) (Peckham et. al. 1973). Females were provisioning nests in all cases where males defended nests and mated. Not only did males defend nests while females were on provisioning trips, but on two occasions, a male was observed to defend a nest while the female was inside the nest. These males were observed to bite at the females, and attempted to pull them out of the nest with their mandibles. One of these males mated with the female when she exited the nest.

Nest defense duration was determined by the length of time a resident male was either in contact with a nest, directly adjacent to a nest, or defending a nest from non-resident males. On day one, males YB, RB and BY, spent a total of 66.7, 21.1, and 12.2 percent of the observation period defending nests, respectively. On day two, males WRB, YB, RY, BB and RB spent a total of 67.3, 41.1, 16.8, 1.2 and 0.8 percent of the observation period defending nests, respectively. Males YB and WRB obtained 71% (5/7) of the observed copulations, and there is a positive correlation between the duration of time which males defend nests and the number of copulations that males obtain; $r = 0.86$.

At times, multiple males were simultaneously defending different nests in the aggregation. Male-male interactions were considered a territorial defense when a resident male flew from his nest to chase a non-resident male. These chases rarely ended in grappling on the ground; otherwise, there was no physical contact. Forty eight aggressive interactions were recorded between resident and non-resident males. Resident males won significantly

more (95%) interactions than non-resident males (Chi-square = 40.1, $df = 2$, $P < 0.001$). In 11 of the 48 interactions, identity and size of both males were known; resident males won 7 of these 11 interactions. Mean head widths of winner and loser males were 3.83mm and 3.76mm, respectively. The difference in mean headwidths between winner and loser males is not statistically significant (t -test = .82, $df = 20$, $P > 0.4$).

DISCUSSION

Size has been demonstrated to determine dominance in territorial sphecids such as *Philanthus* (O'Neill 1983a, b), and in many other insect mating systems (Thornhill and Alcock 1983). In *C. binodis*, however, territory ownership, not size, apparently determines dominance (one should note the small sample size ($n=11$) where identity of both males was known). This phenomenon has also been demonstrated in other insect mating systems (Davies 1978, Eickwort and Ginsberg 1980, Wang and Greenfield 1991). Data also indicate that as the total time invested in nest defense per male increases, the number of copulations obtained per male also increases. This is not surprising, since females mate with the resident male which is defending her nest.

In many *Cerceris* species, females nest in aggregations, but males do not defend nests from conspecific males. The requirement which is likely responsible for the difference between the mating systems of these species and *C. binodis* is that *C. binodis* females retain their receptivity after the initial mating. This might maintain male territoriality, particularly if there is last male sperm precedence (Hook and Matthews 1980, Brockmann and Grafen 1989). However, males in several species of *Philanthus* defend territories which contain nesting females that do not display continuous receptivity (Gwynne 1980, Evans and O'Neill 1988). Data collected from this study do not indicate that fe-

males are continuously receptive throughout the nesting period, only that they mate multiply. In addition, last male sperm precedence is not demonstrated in this species, but often occurs in insects (Thornhill and Alcock 1983).

CONCLUSION

This is the first description of male nest defense in *Cerceris*. This derived mating system shows striking convergence with the mating systems of both *Oxybelus* (Peckham et. al 1973, Hook and Matthews 1980), and *Philanthus* (Evans and O'Neill 1988) species. Moreover, *C. binodis* males do not scent mark territories, and their clypeal brushes are reduced. Since clypeal brushes are a synapomorphy of Philanthinae, and are present in most species of *Cerceris* (Alexander 1992), reduction of the clypeal brushes in *C. binodis* represents a derived condition. Evans and O'Neill (1988) state that scent marking occurs in all territorial philanthines where the mating systems have been described. Therefore, this mating system represents an exception to their statement (see also Alcock and Gamboa 1975).

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Revised Key to the Nearctic Species of *Chrysocharis* Förster (Hymenoptera: Eulophidae), Including Three New Species

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Abstract.—The Nearctic species of *Chrysocharis* are keyed, altogether 63 species. The paper includes the description of three new species: *wahli*, *cornigera*, *sentenaca* and two new combinations from *Chrysocharis* to *Omphale* Haliday: *varia* Hansson, *gracilicornis* Hansson.

The Nearctic and Neotropical species of *Chrysocharis* were revised by Hansson (1987). Sixtyone (61) species were treated and 18 of the species were described as new. From the Nearctic region 57 species were recognized. However, the key for the identification of the species is difficult and laborious to use, mainly because too many characters are used under each item, and characters used in the two alternatives under each item are not always exclusively the same. To improve the key I have rearranged it so that the most obvious characters are used first, and under each item only 1–2 characters are used—only occasionally are more than two characters used. The characters selected are those easy to see and that vary as little as possible. In some cases a species varies in characters used, and this species is found under both alternatives.

In the revised key I have also included changes that has taken place since the publication of the previous key: *Entedon imbrusus* Walker has been transferred to *Chrysocharis* from *Neochrysocharis* Kurdjumov (Hansson in press); the species treated as *Zaommomyia* Girault by Hansson (1986) have been transferred to *Chrysocharis* (Schauff 1991). The three species described as new in this paper are also included. Furthermore, two species regarded as *Chrysocharis* by Hansson (1987) are hereby transferred to *Omphale* Haliday: *gracilicornis* Hansson, *varia* Hansson, both *n. comb.*

The page number after each species in the revised key refers to Hansson (1987). The descriptions, diagnoses, distribution and hosts of Nearctic species of *Chrysocharis* are found in Hansson (1985, 1986, 1987).

RECOGNIZING *CHRYSOCHARIS*

To facilitate the recognition of *Chrysocharis*, following should be helpful. Antenna with apical two segments fused, or with all flagellar segments free (exception: *imbrusus* with three apical segments fused, recognized as a *Chrysocharis* through the long postmarginal vein—1.5× stigmal vein—and antennal scrobes join below frontal suture in female). Clypeus not delimited (exception: *flaviclypeus*, recognized as a *Chrysocharis* through female antennal scrobes that join below frontal suture). Postmarginal vein longer than stigmal vein (exception *wahli* & *cornigera*, recognized as members of *Chrysocharis* through the possession of the three abovementioned characters). Without a sulcus surrounding ocellar triangle (this separates *Chrysocharis* from *Derostenus*).

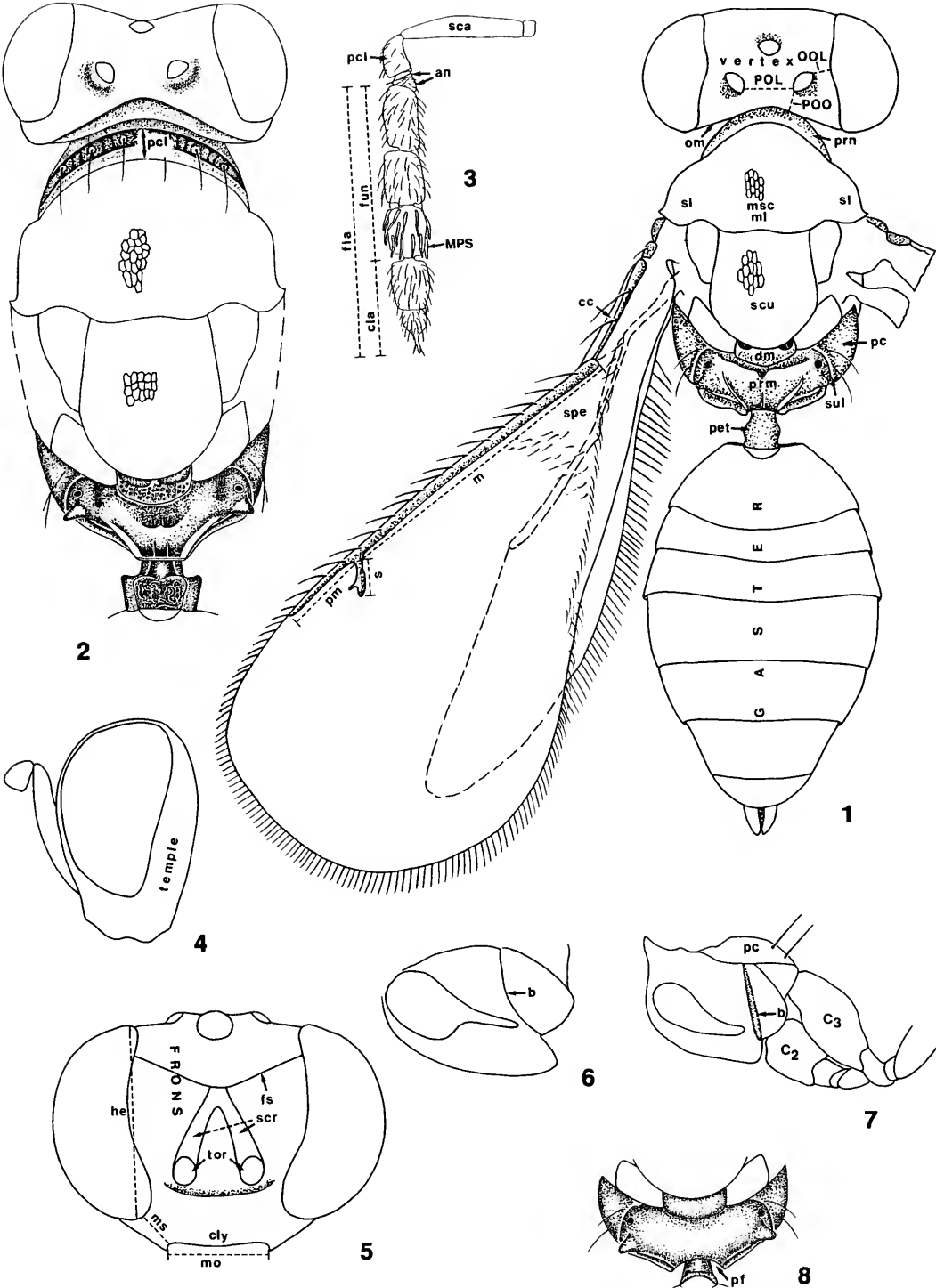
TERMINOLOGY AND ABBREVIATIONS

The terms used in the key and in the text are indicated on Figs 1–8.

Abbreviations of collections: CNC= Canadian National Collection of Insects and Arachnids, Ottawa; LUZM= Lund University Zoological Museum; TAMU= Texas A&M University, College Station.

KEY TO NEARCTIC SPECIES OF *CHRYSOCHARIS*

1. Flagellum with all five segments free (e.g. Figs 35, 39) 2
 - Flagellum with apical two or three segments fused, i.e. the constrictions between the basal funicular segments are narrower than the constrictions between the apical segments (e.g. Figs 37, 38) 19
2. Forewing with a complete row of setae on underside of costal cell (Figs 48, 49) 3
 - Costal cell without row of setae 4
3. Forewing speculum closed (Fig. 49); 5th flagellar segment (including the narrow tip) $1.3\times$ as long as 4th segment (Fig. 35) *C. chilo* (Walker) (female, male) p. 30
 - Forewing speculum open laterally (Fig. 48); 5th flagellar segment $0.9\text{--}1.0\times$ as long as 4th segment (Fig. 36) *C. pilosa* Delucchi (female, male unknown) p. 30
4. Pronotal collar with a transverse carina—at least on median pronotum—parts of pronotum behind carina smooth and shiny (Fig. 87) 5
 - Pronotum without transverse carina, hind margin of pronotum at most with a very narrow smooth strip (Fig. 86) 7
5. Petiole longer than wide (Fig. 62) *C. acoris* (Walker) (female, male) p. 64
 - Petiole at most as long as wide (Figs 56, 59) 6
6. Scape and pedicel bright orange-yellow; clypeus pale yellow *C. illustris* Graham (male) p. 59
 - Scape whitish or pale brown, pedicel brown; clypeus metallic bluish-green *C. occidentalis* (Girault) (female, male) p. 54
7. Propodeal callus with 2 setae 8
 - Propodeal callus with at least 3 setae 14
8. Petiole pale; male flagellar segments with a single whorl of setae at the base of each segment (Fig. 42) *C. beckeri* Yoshimoto (female, male)
 - Petiole dark; male flagellar segments also with setae in middle and at apex 9
9. Propodeum with 2 complete and parallel submedian grooves (Fig. 84) *C. sulcata* (Hansson) (female, male)
 - Propodeum without such grooves 10
10. Forewing speculum open below (Fig. 47) *C. vonones* (Walker) (female, male)
 - Forewing speculum closed below 11
11. Scape bright orange-yellow; reticulation on thoracic dorsum fine and engraved *C. fulviscapus* Hansson (male, female unknown) p. 45
 - Scape whitish or brown; reticulation on thoracic dorsum raised and strong 12
12. Occipital margin with a complete (reaching from eye to eye), high and sharp carina (Fig. 91); frontal suture raised *C. liriomyzae* Delucchi (male) p. 26
 - Occipital margin without a complete carina; frontal suture not raised 13
13. All femora predominantly dark *C. phytomyzivora* Hansson (male) p. 20
 - Femora pale *C. cerodonthae* Hansson (male) p. 21
14. Petiole longer than length of median propodeum (Fig. 85) .. *C. viridis* (Nees) (male) p. 29
 - Petiole at most as long as length of median propodeum 15
15. Postmarginal vein $3.0\text{--}3.5\times$ as long as stigmal vein 16
 - Postmarginal vein $2.0\text{--}2.5\times$ as long as stigmal vein 17
16. Petiole about as long as median propodeum; dorsellum usually excavated and divided in two parts by a median carina and hind part with a median incision (Fig. 69) *C. entedonoides* (Walker) (female, male) p. 28
 - Petiole shorter than median propodeum; dorsellum convex to flat, without median incision and carina (Fig. 63) *C. anyite* (Walker) (female, male) p. 28
17. Hind coxa conspicuously long and slender, about $2.5\times$ as long as wide (Fig. 52); petiolar foramen triangular *C. longicoxa* Hansson (male) p. 26
 - Hind coxa stouter, about $1.5\times$ as long as wide; petiolar foramen semicircular to quadrangular 18

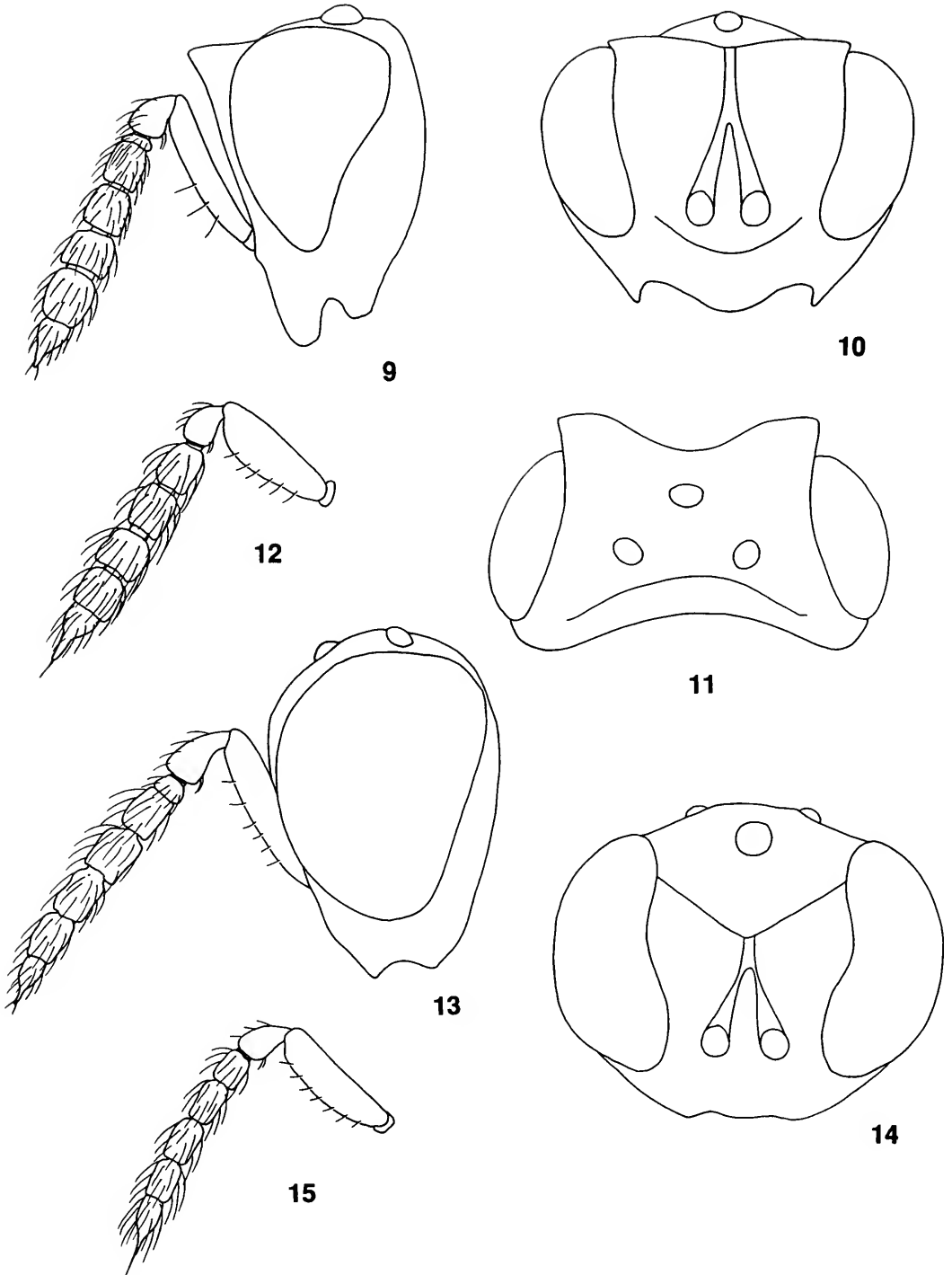


Figs. 1-8. Terminology. 1, *beckeri*, female: cc= costal cell; dm= dorsellum; m= marginal vein; ml= midlobe; msc= mesoscutum; om= occipital margin; OOL= ocell-ocular line; pc= propodeal callus; pet= petiolus; pm= postmarginal vein; POL= postocellar line; POO= distance between hind ocelli and occipital margin; prn=

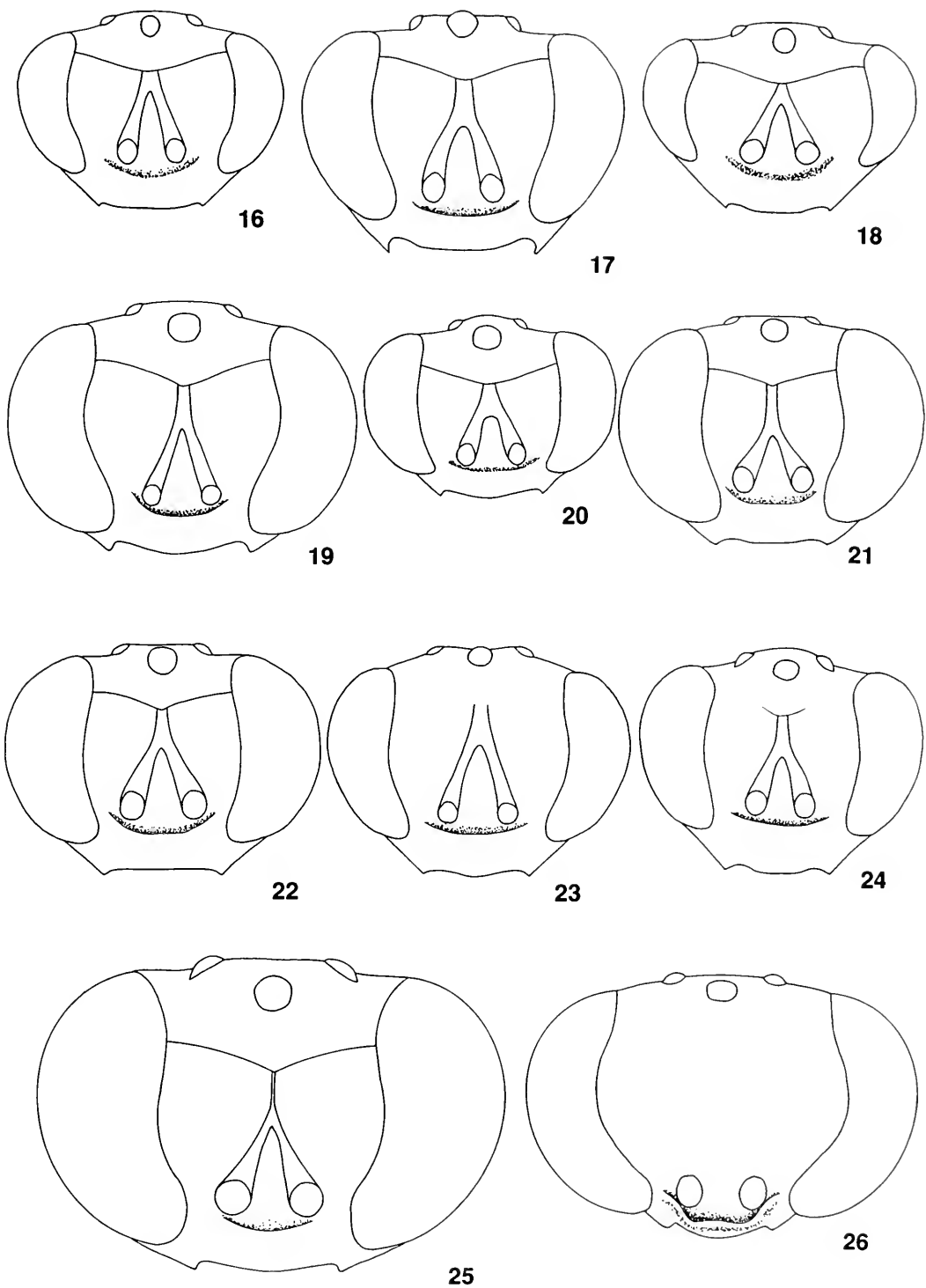
18. Petiole as long as wide (as in Fig. 77); femora usually pale—in a few specimens predominantly dark *C. avia* Hansson (female, male) p. 28
 - Petiole transverse (Fig. 80); femora always predominantly dark *C. phytomyzivora* Hansson (male) p. 20
19. Flagellum with apical three segments fused (Fig. 41) *C. imbrasus* (Walker) (female, male unknown) p. 20
 - Flagellum with apical two segments fused 20
20. Forewing with a complete row of setae on underside of costal cell (as in Figs 48, 49) *C. robusta* Yoshimoto (female, male) p. 62
 - Costal cell without row of setae 21
21. Pronotal collar with transverse carina—at least on median pronotum (Fig. 87) 22
 - Pronotum without transverse carina (Fig. 86) 55
22. Flagellum yellow; frontal suture missing (Fig. 26) *C. walleyi* Yoshimoto (male) p. 60
 - Flagellum brown; frontal suture present 23
23. Petiole at least 1.5× as long as wide 24
 - Petiole at most as long as wide 26
24. Malar space very narrow, 1/15 the width of mouth opening (Fig. 92); frontal suture smoothly curved; with a procession between antennal toruli *C. prodice* (Walker) (female, male) p. 65
 - Malar space not as narrow, 1/7 the width of mouth opening (Fig. 93); frontal suture more straight; without procession between toruli 25
25. Occipital margin with a low sharp carina; propodeal callus with 2 (3) setae; female frons above fork usually with rather strong reticulation; male frons smooth or with weak reticulation *C. acoris* (Walker) (female, male) p. 64
 - Occipital margin rounded and smooth (in a few cases with a very weak carina); propodeal callus with 4–5 (3) setae; female frons above fork smooth or with very weak reticulation (male unknown) *C. amasis* (Walker) (female) p. 65
26. Propodeum with a strong and complete median carina (Fig. 58) *C. walleyi* Yoshimoto (female) p. 60
 - Propodeum without a complete median carina 27
27. Posteromedian part of propodeum with two submedian, slightly curved carinae (Fig. 70); male pedicel bright orange-yellow *C. gemma* (Walker) (female, male) p. 59
 - Posteromedian propodeum without carinae, or with 2–6 short and straight carinae (e.g. Fig. 73); male pedicel brown or whitish 28
28. Anteromedian part of propodeum with a wide and strong median carina—reaching half the length of propodeum and then dividing into 2 weaker carinae which diverge towards the hind edge of propodeum (Fig. 73) *C. illustris* Graham (female) p. 59
 - Median carina on anteromedian part of propodeum weaker or missing 29
29. Clypeus partly or completely pale yellow 30
 - Clypeus completely dark and metallic 31
30. Reticulation on thoracic dorsum very dense and strong, almost like punctulation; propodeal callus with 5 setae *C. flaviclypeus* Hansson (female, male unknown) p. 63

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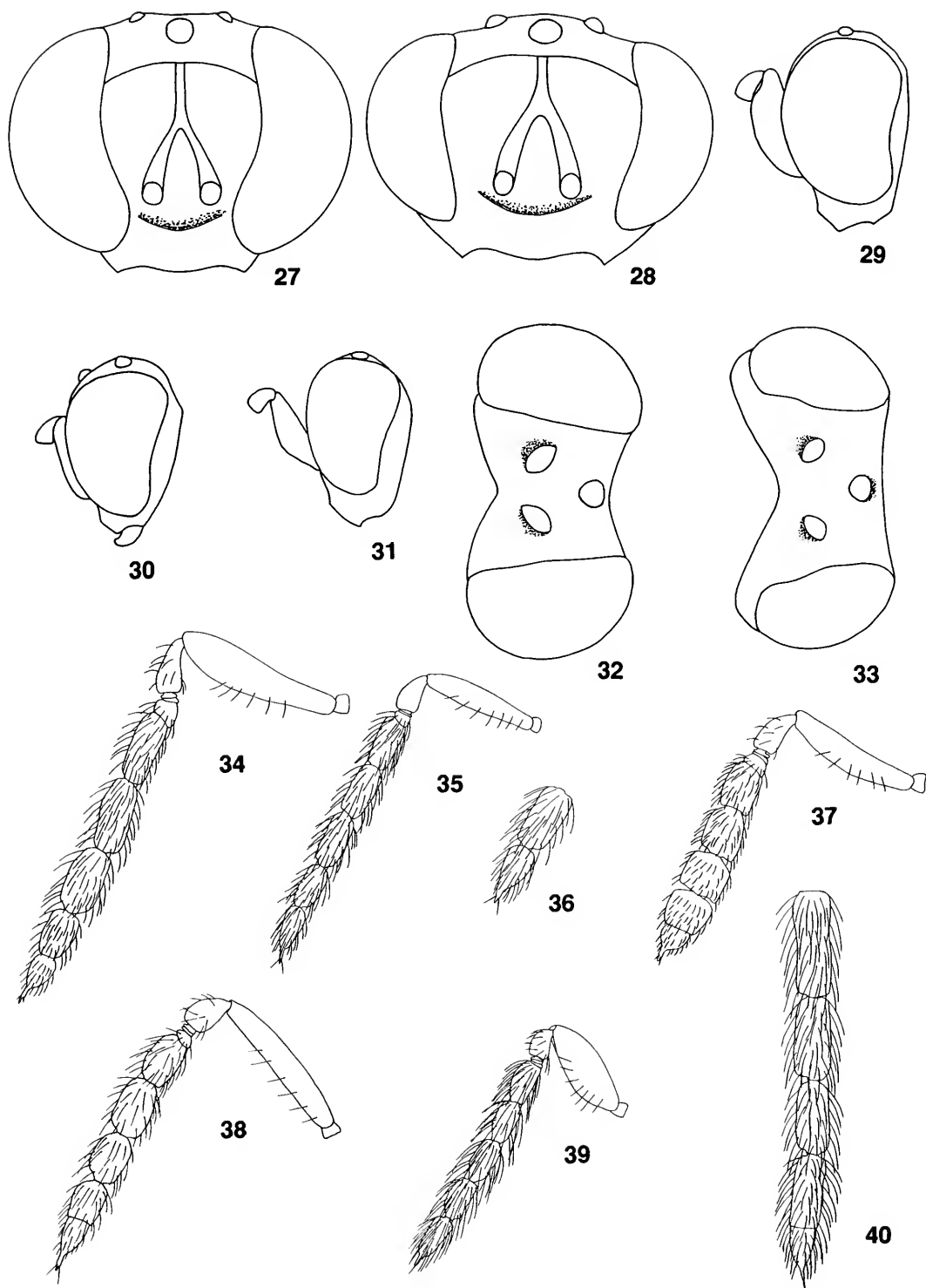
propodeum; prn= pronotum; s= stigmal vein; scu= scutellum; sl= sidelobe; spe= speculum; sul= spiracular sulcus. 2, *collaris*, female: pcl= pronotal collar. 3, Antenna, *compressicornis*, female: an= anelli; cla= clava; fla= flagellum; fun= funiculus; MPS= multiporous plate sensilla; pcl= pedicel; sca= scape. 4, Head, side view, *phytomyzivora*, female. 5, Head, front view, *clarkae* male: cly= clypeus; fs= frontal suture; he= height of eye; mo= width of mouth opening; ms= width of malar space; scr= antennal scrobes; tor= antennal toruli. 6, Mesothorax, side view, *longicoxa*, female: b= borderline between upper and lower mesepimeron. 7, Meso+metathorax, side view, *tristis*, female: b= as in Fig. 6; c₂= mid coxa; c₃= hind coxa; pc= propodeal callus. 8, *mediana*, female: pf= petiolar foramen.



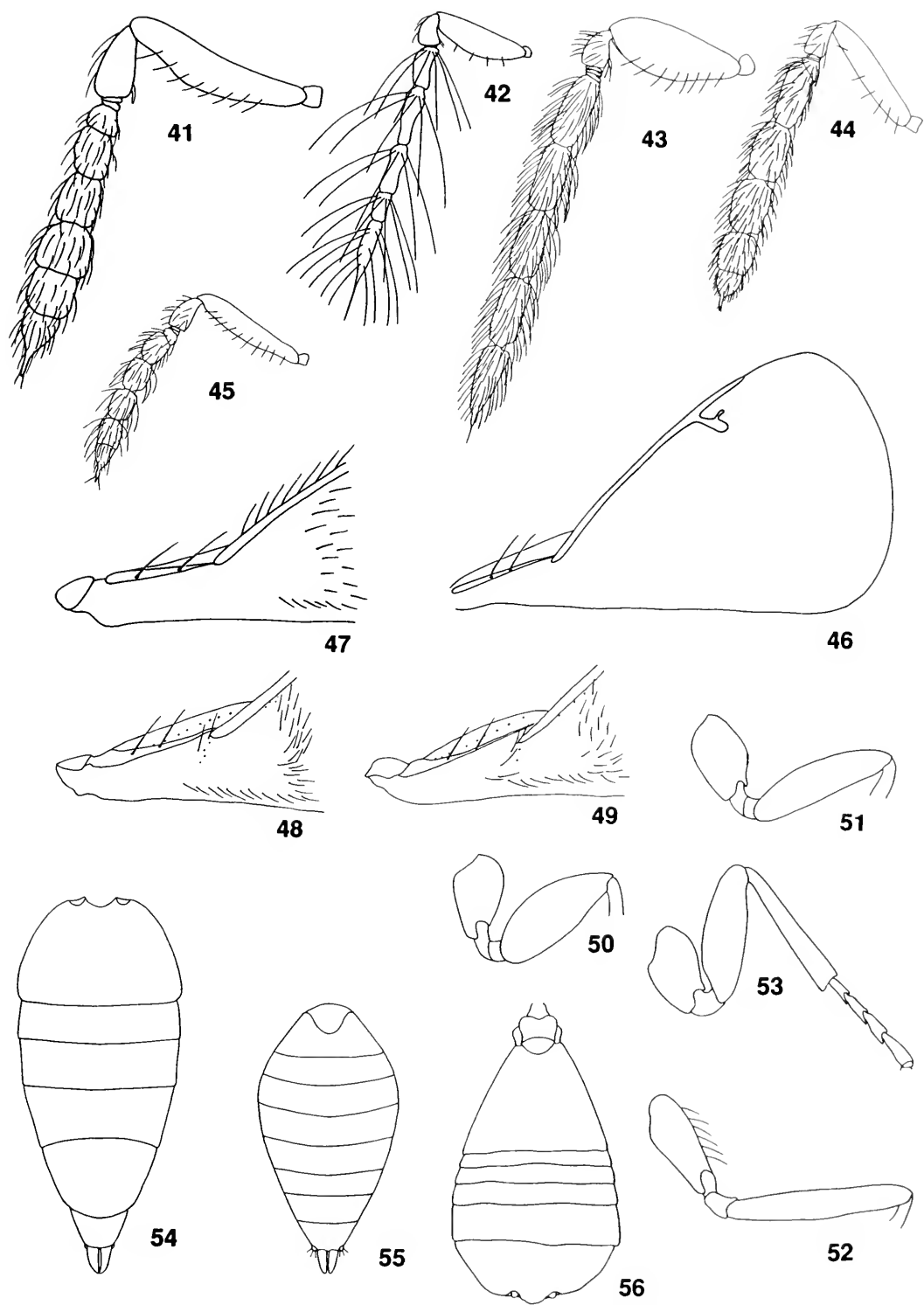
Figs. 9–15. *Chrysocharis* n.spp. 9–12. *cornigera*. 9, Head, side view, female. 10, Head, front view, female. 11, Head, dorsal view, female. 12, Antenna, male. 13–15. *wahlhi*. 13, Head, side view, female. 14, Head, front view, female. 15, Antenna, male.



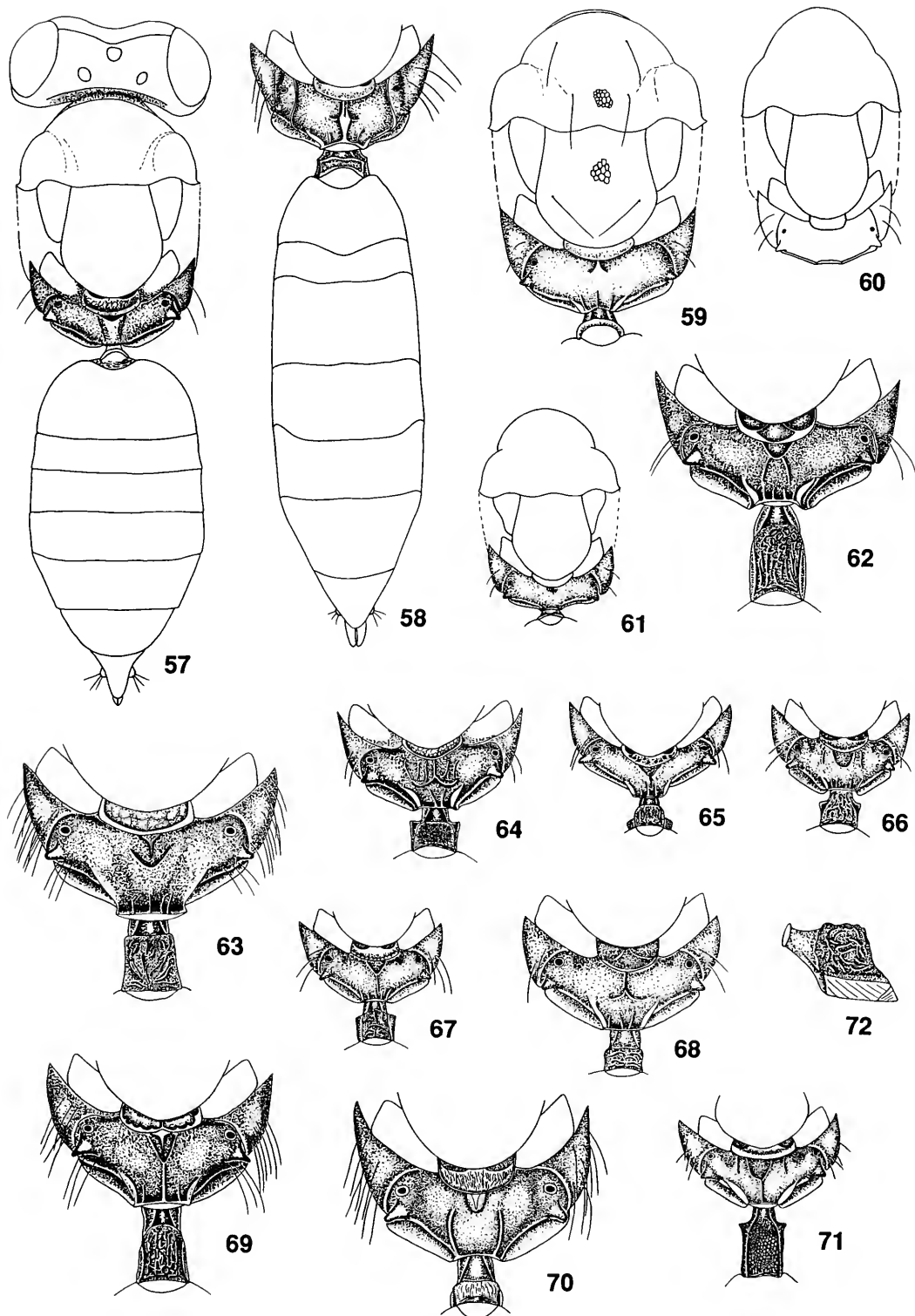
Figs. 16–26. Head, front view. 16–17, *ainsliei*, female. 18, Ditto, male. 19, *oscinidis*, female. 20, Ditto, male. 21, *chromatomyiae*, female. 22, Ditto, male. 23, *perditor*, female. 24, Ditto, male. 25, *amasis*, female. 26, *walleyi*, male.



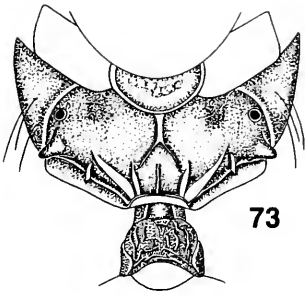
Figs. 27–40. 27, Head, front view, *tristis*, female. 28, Ditto male. 29, Head, lateral view, *coptodiscae*, male. 30, Ditto, *pallidigaster*, female. 31, Ditto, *submutica*, male. 32, Head, dorsal view, *occidentalis*, female. 33, Ditto, *coptodiscae*, female. 34–40. Antennae. 34, *occidentalis*, female. 35, *chilo*, female. 36, Apical 2 flagellar segments, *pilosa*, female. 37, *coptodiscae*, female. 38, *lirionyzae*, female. 39, Ditto, male. 40, Flagellum, *compressicornis*, male.



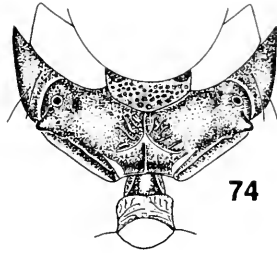
Figs. 41-56. 41-45. Antennae. 41, *imbratus*, female. 42, *beckeri*, male. 43, *pubens*, male. 44, *polyzo*, female. 45, *prodice*, female. 46, Forewing, *paradoxa*. 47-49. Base of forewing. 47, *vonones*. 48, *pilosa*. 49, *chilo*. 50-52. Hindleg from coxa to basal tibia. 50, *occidentalis*. 51, *coptodiscus*. 52, *longicoxa*. 53, Hindleg, *polita*. 54, Gaster, *laomedon*, female. 55, Ditto, *longigaster*, female. 56, Petiole + gaster, *illustris*, male.



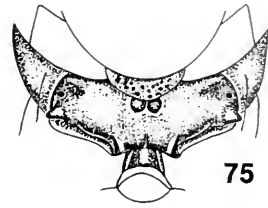
Figs. 57-72. 57, Body, dorsal view, *acutigaster*, female. 58, Propodeum+petiole+gaster, *walleyi*, female. 59-61. Mesosoma+petiole, female. 59, *occidentalis*. 60, *mediana*. 61, *polita*. 62-71. Propodeum+petiole, female. 62, *acoris*. 63, *amygite*. 64, *assis*. 65, *cerodonthae*. 66, *chromatomyiae*. 67, *clarkae*. 68, *crassiscapus*. 69, *entedonoides*. 70, *gemma*. 71, *giraulti*. 72, Petiole, side view, *clarkae*.



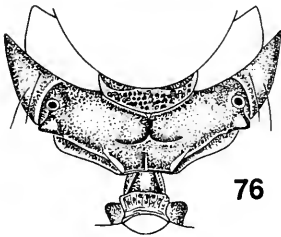
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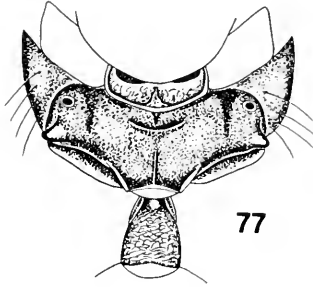
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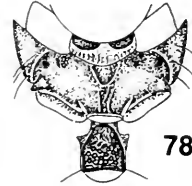
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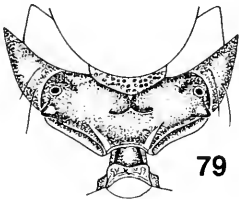
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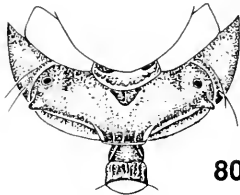
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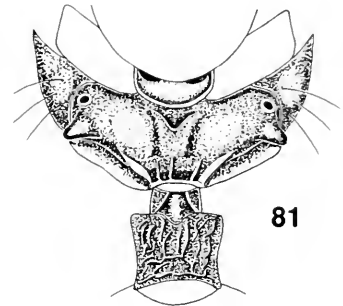
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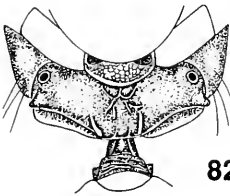
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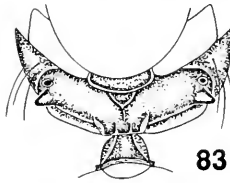
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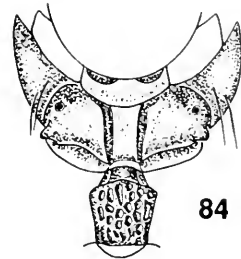
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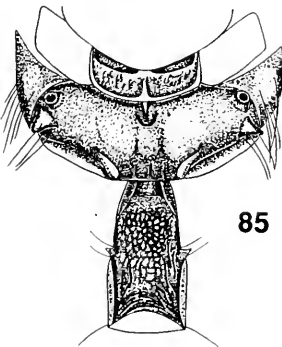
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Figs. 73–85. Propodeum+petiole, female. 73, *illustris*. 74, *laricinellae*. 75, *nephereus*. 76, *nitetis*. 77, *orbicularis*. 78, *oscinidis*. 79, *pentheus*. 80, *phytomyzivora*. 81, *polyzo*. 82, *pubicornis*. 83, *purpurea*. 84, *sulcata*. 85, *viridis*.

- Reticulation on thoracic dorsum weak; propodeal callus with 2 setae *C. aluta* Yoshimoto (female, male) p. 58
- 31. Anteromedian part of propodeum with a round to triangular fovea bordered by a raised edge (Fig. 83), fovea not divided by a median carina; propodeal callus with 3–4 setae *C. purpurea* Bukowski (female, male) p. 58
- Anteromedian part of propodeum either with carinae shaped like a V, Y or a T (turned upside-down) (e.g. Figs 74, 76), or with two submedian pits (e.g. Fig. 75); propodeal callus with 2 setae 32
- 32. Females, i.e. gaster widest close to base or in the middle and with apex pointed or rounded (e.g. Figs 1, 54), scape comparatively narrow, $4.3\text{--}5.1\times$ as long as wide 33
- Males, i.e. gaster narrow at base and gradually becoming wider towards apex (Fig. 56), scape comparatively wide, $3.1\text{--}3.3\times$ as long as wide 45
- 33. Gaster long—ratio length of mesosoma/length of gaster = $0.6\text{--}0.7$ —more or less parallel-sided and with hind part pointed (Fig. 54) 34
- Gaster shorter—ratio m/g at the lowest 0.8 but usually 1.0—and oval-shaped with hind part rounded 35
- 34. Malar space very narrow—about $1/8$ the width of mouth opening (Fig. 97); fore coxa predominantly pale *C. laomedon* (Walker) p. 57
- Malar space wider—about $1/4$ the width of mouth opening; fore coxa dark and metallic *C. elongata* (Thomson) (male unknown) p. 56
- 35. Scutellum with engraved reticulation; flagellum stout, flagellar segments gradually becoming shorter and wider towards apex (Fig. 37) *C. coptodiscae* Yoshimoto p. 53
- Scutellum with raised reticulation; flagellum slender (e.g. Fig. 34) 36
- 36. Scutellum flattened; anteromedian part of propodeum with two submedian pits (Fig. 75) *C. nephereus* (Walker) p. 52
- Scutellum convex; anteromedian part of propodeum with carinae shaped like a V, Y or a T 37
- 37. Transverse pronotal carina weak and present only on median part of pronotum 38
- Transverse pronotal carina strong and present along the major part of pronotum 40
- 38. Hind femur conspicuously stout, $2.5\times$ as long as wide (Fig. 50); malar space narrower than width of scape *C. occidentalis* (Girault) p. 54
- Hind femur slender, $4.0\times$ as long as wide (as in Fig. 51); malar space at least as wide as width of scape 39
- 39. Malar space as wide as width of scape (Fig. 30); frons below suture golden-red *C. pallidigaster* Hansson p. 49
- Malar space $1.5\text{--}2.0\times$ as wide as width of scape (Fig. 31); frons below suture usually purple *C. submutica* Graham p. 49
- 40. Malar space narrower than the width of scape 41
- Malar space at least as wide as width of scape 42
- 41. Petiole as long as wide, with protruding forecorners (Fig. 64) *C. assis* (Walker) p. 64
- Petiole transverse, without protruding forecorners (as in Fig. 79) *C. paradoxa* Hansson p. 58
- 42. Pronotal collar long (Fig. 2); occipital margin with a carina behind ocellar triangle *C. collaris* Graham p. 52
- Pronotal collar shorter (Fig. 87); occipital margin without carina 43
- 43. Meshes of reticulation with about the same size over entire frons (Fig. 95); scutellum distinctly elongate—ratio length/width = 1.2 *C. laricinellae* (Ratzeburg) p. 50
- Reticulation on frons below suture usually with larger meshes than on frons above suture (as in Fig. 96); scutellum about as long as wide 44
- 44. Raised surface of petiole small (Fig. 79); hind femur completely white or very pale brown at base *C. pentheus* (Walker) p. 51

- Raised surface of petiole larger (Fig. 76); hind femur usually predominantly dark *C. nitetis* (Walker) p. 51
- 45. Third anellus large (e.g. as in Fig. 37) *C. assis* (Walker) p. 64
 - Third anellus small and discoid 46
- 46. Gaster with a pale subbasal spot *C. pallidigaster* Hansson p. 49
 - Gaster without a pale subbasal spot 47
- 47. Malar space narrow—about 0.3× as wide as width of scape 48
 - Malar space wider—at least 0.5× as wide as width of scape 49
- 48. Propodeum with a complete median carina or with 2 weak, complete and parallel carinae *C. laomedon* (Walker) p. 57
 - Propodeum without longitudinal carinae *C. paradoxa* Hansson p. 58
- 49. Transverse carina along pronotum present and complete 50
 - Transverse carina along pronotum weak and incomplete 54
- 50. Scutellum flattened and about as long as wide; reticulation on scutellum small-meshed (Fig. 88) *C. nephereus* (Walker) p. 52
 - Scutellum distinctly longer than wide 51
- 51. Forewing subtruncate (as in Fig. 46) *C. paradoxa* Hansson p. 58
 - Forewing rounded apically 52
- 52. Eyes 4.5× as high as width of malar space (Fig. 94) *C. laricinellae* (Ratzeburg) (spring generation) p. 50
 - Eyes 5–7× as high as malar space (as in Fig. 96) 53
- 53. Entire frons with small-meshed reticulation (as in Fig. 95) *C. laricinellae* (summer generation) p. 50
 - Frons below suture with larger meshes than above suture (Fig. 96) *C. pentheus/C. nitetis* (inseparable) p. 51
- 54. Malar space as wide as width of scape; temples comparatively large and eyes comparatively small, width of temples at lower edge of eyes 0.15× the height of an eye (Fig. 31) *C. submutica* Graham p. 49
 - Malar space only 0.5× as wide as width of scape; temples smaller and eyes larger, width of temples at lower edge of eyes 0.07× the height of an eye (Fig. 29) *C. nephereus/C. coptodisciae* (inseparable) p. 52–53
- 55. Propodeum with two complete parallel submedian grooves (Fig. 84) *C. sulcata* (Hansson) (female, male)
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- 56. Petiole distinctly longer than wide (at least 1.4× as long as wide) 57
 - Petiole usually at most as long as wide 63
- 57. Frontal suture absent (Figs 23, 24) *C. perditor* Hansson (female, male) p. 38
 - Frontal suture present 58
- 58. Petiole with a pair of medio-lateral horns (Fig. 85); propodeum with 2–5 setae inside spiracular sulci *C. viridis* (Nees) (female) p. 29
 - Petiole with a pair of antero-lateral horns (Fig. 71); propodeum without setae inside spiracular sulci 59
- 59. Scape completely pale; postmarginal vein only 1.3× as long as stigmal vein *C. gibsoni* Hansson (female, male) p. 38
 - Scape with at least apical part infuscate; postmarginal vein 2× as long as stigmal vein 60
- 60. Frontal suture down-curved (Figs 27, 28); speculum open below (as in Fig. 47) *C. tristis* Hansson (female, male) p. 41
 - Frontal suture curved upwards or straight; speculum closed below (a few specimens have an open speculum) 61
- 61. Petiole at least 2× as long as wide *C. ignota* Hansson (female, male) p. 39
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- 62. Dorsellum comparatively short and wide, 6.5× as wide as long (Fig. 71); dorsal surface of petiole concave in sideview *C. giraulti* Yoshimoto (female, male) p. 35

- Dorsellum longer, 3× as wide as long (Fig. 78); dorsal surface of petiole straight in sideview *C. oscinidis* Ashmead (female, male) p. 34
- 63. Petiole pale, as long as wide 64
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- 64. Frontal suture almost straight; thoracic dorsum with weak reticulation *C. minuta* (Hansson) (female, male)
 - Frontal suture V-shaped; thoracic dorsum with strong reticulation *C. beckeri* Yoshimoto (female, male)
- 65. Clypeus pale yellow *C. flaviclypeus* Hansson (female, male unknown) p. 63
 - Clypeus dark and metallic 66
- 66. Mouth opening wider than height of an eye—ratio width of mouth/height of eye= 1.1 *C. kimamaensis* Hansson (female, male unknown) p. 45
 - Mouth opening narrower than height of an eye 67
- 67. Lateral parts of frontal suture raised to form two conspicuous horns (Figs 9–11) *C. cornigera* n.sp. (female, male)
 - Frontal suture not raised, or in one species (*Iiriomyzae*) with entire frontal suture slightly raised 68
- 68. Anteromedian part of propodeum without carinae, a fold or a pit (e.g. Fig. 8) 69
 - Anteromedian part of propodeum with carinae, a fold or a pit 72
- 69. Propodeum with a complete median carina *C. vonones* (Walker) (female, male)
 - Propodeum smooth, without median carina 70
- 70. Forewing with an infusate spot below stigmal vein; postmarginal vein as long as stigmal vein; male pedicel pale *C. wahlili* n.sp. (female, male)
 - Forewing hyaline; postmarginal vein twice as long as stigmal vein; male pedicel dark 71
- 71. All femora usually predominantly dark and metallic; hind femur comparatively slender, 3.5× as long as wide; mesosoma comparatively slender, 1.6× as long as wide (Fig. 60) *C. mediana* Förster (female, male) p. 48
 - Femora completely pale; hind femur conspicuously stout, 3.2× as long as wide (Fig. 52); mesosoma comparatively stouter, 1.4× as long as wide (Fig. 61) *C. polita* (Howard) (female, male) p. 48
- 72. Anteromedian part of propodeum with a single median pit (e.g. Figs 57, 67, 78) 73
 - Anteromedian part of propodeum with carinae shaped like a Y or a T (turned upside-down) (e.g. Fig. 68), a fold (e.g. Fig. 59), two submedian pits (e.g. Fig. 75), or a raised peak 88
- 73. Petiole very short, less than half as long as wide (Figs 8, 57) 74
 - Petiole longer, at least as long as wide (e.g. Figs 78, 81) 76
- 74. Hind part of anteromedian fovea on propodeum considerably raised; female with antennal clava distinctly wider than first 2 funicular segments *C. acutigaster* Hansson (female, male) p. 22
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- 75. All femora usually predominantly dark and metallic; hind femur comparatively slender, 3.5× as long as wide; mesosoma comparatively slender, 1.6× as long as wide (Fig. 60) *C. mediana* Förster (female, male) p. 48
 - Femora completely pale; hind femur conspicuously stout, 3.2× as long as wide (Fig. 52); mesosoma comparatively stouter, 1.4× as long as wide (Fig. 61) *C. polita* (Howard) (female, male) p. 48
- 76. Anteromedian fovea on propodeum very wide—several times wider than long (as in Fig. 1) *C. vonones* (female, male)
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- 77. Borderline between upper and lower mesepimeron straight (Fig. 7); petiolar foramen with a large membrane in upper part (Fig. 77) 78

- Borderline between upper and lower mesepimeron at least slightly curved (Fig. 6); petiolar foramen with a very small membrane in upper part, or without membrane 81
- 78. All coxae pale—fore coxa sometimes infuscate in upper half *C. subcircularis* Yoshimoto (female, male) p. 33
- At least some, usually all coxae dark and metallic 79
- 79. Forewing with speculum open below (as in Fig. 47); female gaster long—ratio length of mesosoma/length of gaster= 0.8, with hind part pointed (Fig. 55) *C. longigaster* Hansson (female, male unknown) p. 32
- Forewing with speculum closed; female gaster shorter—ratio length of mesosoma/length of gaster= 1.2–1.3, with hind part less pointed 80
- 80. Eyes comparatively small, height of eye 4.0–7.0× the width of malar space in female, 2.6× in male (Figs 16–18); femora usually predominantly dark, but occasionally pale; postmarginal vein frequently less than 2× as long as stigmal vein *C. ainsliei* Crawford (female, male) p. 31
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- 81. Frontal suture raised; with an interantennal process between toruli (Fig. 89); mouth opening with an incision below eye (Fig. 90) *C. liriomyzae* Delucchi (female) p. 26
- Frontal suture not raised; without process between toruli; mouth opening without incision 82
- 82. Petiole with raised surface quadrangular (Fig. 81) (shape varying from trapezoid, quadratic to rectangular) *C. polyzo* (Walker) (female, male) p. 22
- Raised surface of petiole not quadrangular (e.g. Figs 66, 67) 83
- 83. Hind coxa long and slender, about 2.5× as long as wide (Fig. 52); propodeal callus with 5–8 setae; petiolar foramen triangular *C. longicoxa* Hansson (female, male) p. 26
- Hind coxa stouter, about 1.5× as long as wide; propodeal callus with 2–4 (some specimens of *clarkae* have 5) setae; petiolar foramen rounded or quadrangular 84
- 84. Flagellum thick, about 2× as wide as width of scape (Figs 3, 40); each flagellar segment with MPS in two transverse rows *C. compressicornis* Ashmead (female, male) p. 16
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- Petiole without protruding forecorners, shorter (Figs 65, 80) 87
- 86. Raised surface of petiole considerably raised, with coarse sculpture—which is situated at a much higher level than protruding forecorners (Fig. 72); propodeal callus with 3 (4–5) setae *C. clarkae* Yoshimoto (female, male) p. 23
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- 87. Femora predominantly dark *C. phytomyzivora* Hansson (female) p. 20
- Femora pale *C. cerodonthae* Hansson (female) p. 21
- 88. Anteromedian part of propodeum raised in a peak; hind coxa long and slender, 2.5× as long as wide (Fig. 52) *C. longicoxa* Hansson (female, male) p. 26
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- Without median groove on mesoscutum and scutellum 90
- 90. Propodeal callus with 3–4 setae *C. pubicornis* (Zetterstedt) (female, male) p. 16
- Propodeal callus with 2 setae 91

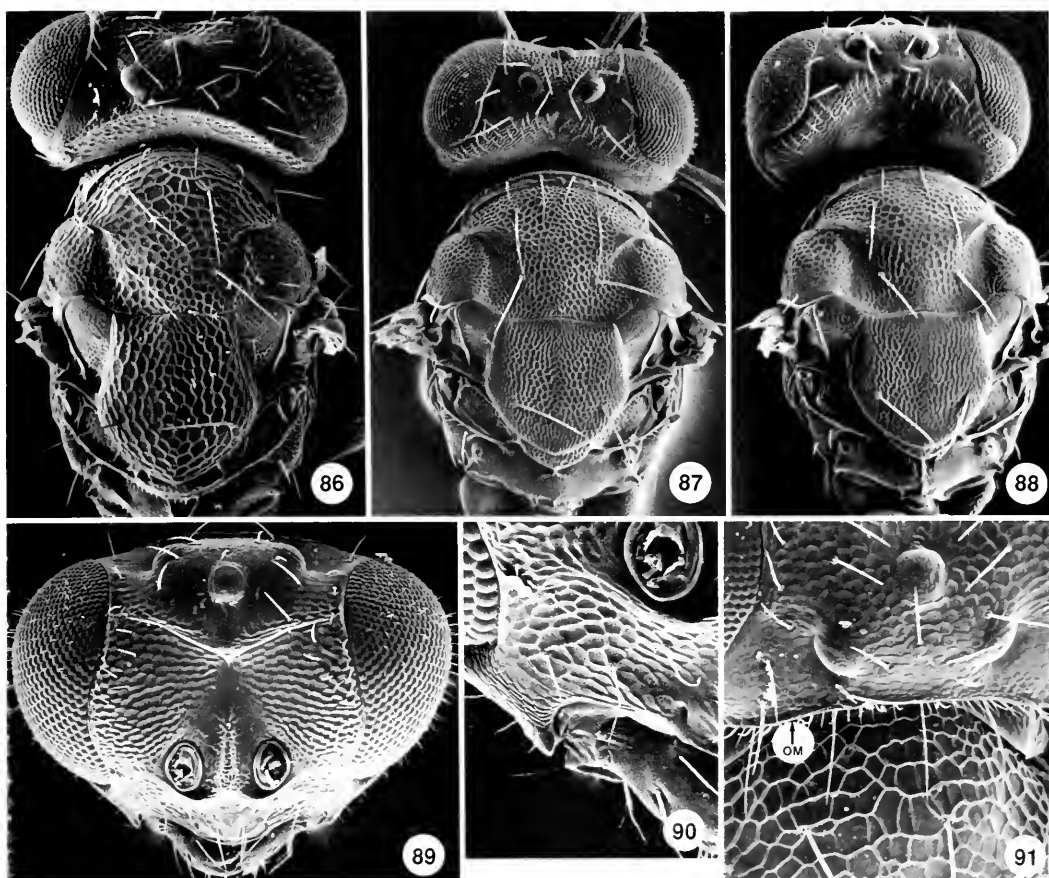
91. Flagellum thick, about $2\times$ as wide as width of scape (Figs 3, 40); each flagellar segment with MPS in two transverse rows *C. compressicornis* Ashmead (female, male) p. 16
 – Flagellum more slender, at most $1.5\times$ as wide as width of scape; each flagellar segment with MPS in one transverse row 92
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 – Hind femur slender, $3.9\times$ as long as wide (as in Fig. 51); malar space at least as wide as width of scape 95
95. Malar space $1.5\text{--}2\times$ as wide as width of scape 96
 – Malar space as wide as width of scape 98
96. Postmarginal vein only $1.3\times$ as long as stigmal vein *C. gemina* Hansson p. 56
 – Postmarginal vein $2\times$ as long as stigmal vein 97
97. Eyes and ocelli larger, ratio height of eye/width of mouth = 2.1, distance between hind ocelli $2\times$ width of one ocellus *C. submutica* Graham p. 49
 – Eyes and ocelli smaller, ratio height of eye/width of mouth = 1.7, distance between hind ocelli $3.4\times$ width of one ocellus *C. sentenaca* n.sp.
98. Borderline between upper and lower mesepimeron curved (as in Fig. 6)
 *C. griffithsi* Hansson p. 17
 – Borderline between upper and lower mesepimeron straight (as in Fig. 7) 99
99. Scutellum flattened (Fig. 87) *C. nephereus* (Walker) p. 52
 – Scutellum convex *C. pallidigaster* Hansson p. 49
100. Gaster with a pale subbasal spot *C. pallidigaster* Hansson p. 49
 – Gaster without a pale subbasal spot 101
101. Hind pair of ocelli close, distance between them $0.9\times$ the largest measure of one ocellus (Fig. 32) *C. occidentalis* (Girault) p. 54
 – Hind pair of ocelli further apart, distance between them $2\times$ the largest measure of one ocellus (as in Fig. 33) 102
102. Malar space as wide as width of scape 103
 – Malar space $0.5\times$ as wide as width of scape 104
103. Thoracic dorsum convex; ocelli larger, distance between hind ocelli $1.8\times$ width of one ocellus *C. submutica* Graham p. 49
 – Thoracic dorsum flat; ocelli smaller, distance between hind ocelli $3.5\times$ width of one ocellus *C. sentenaca* n.sp.
104. Scutellum convex and $1.4\times$ as long as wide; borderline between upper and lower mesepimeron curved (as in Fig. 6) *C. griffithsi* Hansson p. 17
 – Scutellum flattened and about as long as wide; borderline between upper and lower mesepimeron straight (as in Fig. 7) *C. nephereus* (Walker) p. 52

DESCRIPTIONS

Chrysocharis wahli n. sp. Figs 13–15

Type material.—Holotype female labelled “USA: California, Santa Barbara County, 18 mi. WNW Cuyama (T11N,

1228W, sect. 32), 1–7.iii.88, W.E. Wahl, MT”, in CNC. Paratypes: 5 females with same label-data as holotype; 3 females “USA: California, San Luis Obispo County, 6 mi SE Pozo, 1500’, 26.iii–9.iv.90, W.E. Wahl”; 1 female 2 males with same label as previous but collected 9–21.iv.90; 3 fe-



Figs. 86–91. 86–88. Head+mesosoma, dorsal view. 86, *lirionomyzae*, female. 87, *nephereus*, female. 88, Ditto, male. 89–91. *lirionomyzae*. 89, Head, front view. 90, Semicircular incision in lateral part of mouth opening. 91, Occipital margin (om).

males in LUZM, remaining in CNC; 1 male "USA: California, San Bernardino County, Summit Valley, 2mi. E Hwy 15, 28.v.1981, J Woolley 81/025" (TAMU).

Etymology.—Named after W.E. Wahl, who ran malaise-traps in California and thereby collected a large material of use to me and other taxonomists.

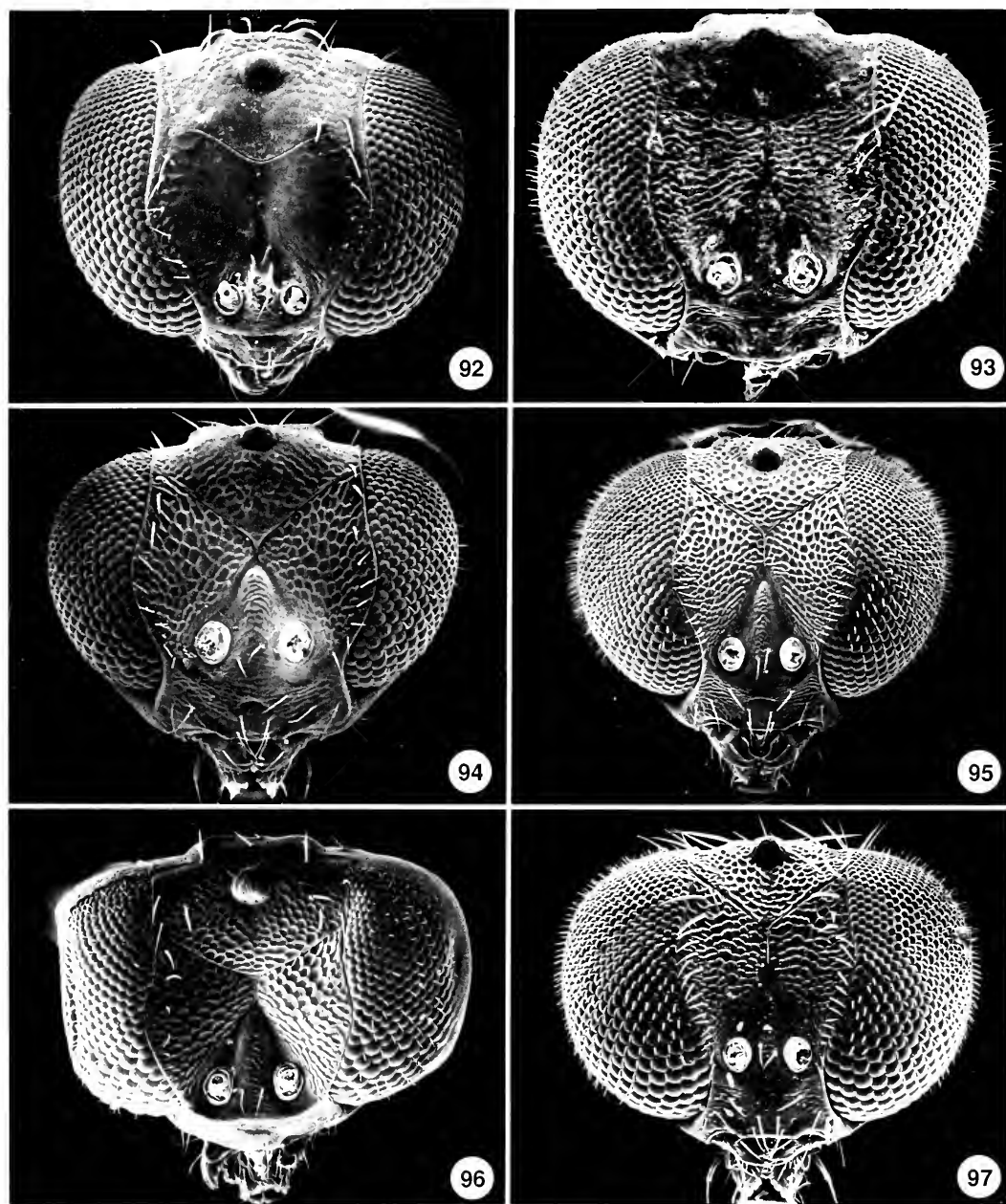
Diagnosis.—Forewing with an infusate spot below stigmal vein; postmarginal vein short, as long as stigmal vein; anteromedian part of propodeum smooth; male pedicel pale.

Description.—Length of body: Female = 1.2–1.6 mm, male = 0.9 mm.

Head: Scape pale, remaining antenna

dark; male pedicel pale. Apical 2 segments of flagellum fused (Figs 13, 15). HE/MS/MO female: 4.6/1.0/2.2, male: 3.0/1.0/1.9. Malar space 1.5× as wide as width of scape in both sexes. Frons golden-green, with strong and small-meshed reticulation. Frontal suture V-shaped. Vertex metallic greenish-blue, with strong and small-meshed reticulation. Inner orbit of eye with 1 row of setae. POL/OOL/POO: 2.2/1.0/1.2. Occipital margin rounded. Ratio width of head/width of thorax across posterior mesoscutum = 1.1.

Mesosoma: Pronotum without transverse carina. Mesoscutum and scutellum metallic greenish-blue; with strong and



Figs. 92-97. Head, front view. 92, *prodice*, female. 93, *amasis*, female. 94, *laricinellae*, male, spring generation. 95, Ditto, female, summer generation. 96, *pentheus*, male. 97, *laomedon*, female.

small-meshed reticulation; scutellum flattened and about as long as wide. Dorsellum small and convex, $3.4\times$ as wide as long, with strong reticulation. Borderline between lower and upper mesepimeron

weakly curved. All coxae dark and metallic (fore coxa in some specimens pale with darkmetallic base) with weak reticulation; femora and tibiae pale; tarsi pale with 4th segment dark. Forewing with an infusate

spot below stigmal vein, rounded with speculum closed, and with a narrow costal cell. Ratios length of M/PM/S: 4.4/1.0/1.0. Propodeum golden-green; anteromedian part smooth; surface with weak reticulation; propodeal callus with 2 setae. Petiolar foramen semicircular.

Metasoma: Petiole very short, in dorsal view visible only as a narrow and smooth strip (as in Fig. 75). Gaster golden-green or golden-purple; male with a small pale subbasal spot; with strong and small-meshed reticulation; oval-shaped in female. Ratio length of mesosoma/length of gaster female = 0.8–0.9, male = 1.0–1.2.

Distribution.—USA (California).

Remarks.—This species belongs in the *mediana*-group, it shares the narrow costal cell in forewing and the smooth anteromedian part of propodeum with the other species in the group.

Chrysocharis cornigera n. sp.

Figs 9–12

Type material.—Holotype female labelled "Canada: Alberta, 14 km S S. Saskatchewan River, 1.vi.1981, Thormin, Reney & Brouwer, sand dune complex", in CNC. Paratypes: 8 females 12 males with same label-data as holotype, 3 females 5 males in coll. LUZM, remaining in CNC.

Etymology.—*cornigera* is latin and means "with horns".

Diagnosis.—Lateral parts of frons, including frontal suture, considerably raised to form 2 conspicuous horns (Figs 9–11); clypeus semicircularly protruding; mouth opening with a semicircular incision below eye-mandibles are possible to point straight forward when fitted in these incisions; postmarginal vein short, as long as stigmal vein; propodeal callus with three setae.

Description.—Length of body: Female = 0.9–1.3 mm, male = 1.1–1.3 mm.

Head: Entire antenna dark. Flagellum with 2 apical segments fused (Figs 9, 12). HE/MS/MO female: 4.8/1.0/3.6, male: 2.8/1.0/2.3. Clypeus semicircularly pro-

truding; mouth opening with a semicircular incision below eye. Malar space 1.5× as wide as width of scape in both sexes. Frons below suture golden-purple in female, golden-green in male, both sexes with weak reticulation. Frontal suture straight; lateral parts of frons, including frontal suture, considerably raised to form 2 conspicuous horns (Figs 9–11). Frons above suture and vertex golden-green, golden-red or golden-blue, with weak reticulation. Inner orbit of eye with 1 row of setae. POL/OOL/POO: 2.6/1.8/1.0. Occipital margin with a weak edge. Ratio width of head/width of thorax across posterior mesoscutum = 1.2.

Mesosoma: Pronotum without transverse carina. Mesoscutum and scutellum golden-green, golden-blue or golden-red—scutellum in some specimens with anterior half purplish; with rather strong to weak reticulation. Dorsellum convex to flat, smooth and with 2 anterolateral foveas. Borderline between lower and upper mesepimeron straight. All coxae dark and metallic with strong reticulation. Femora with basal $\frac{1}{2}$ to $\frac{2}{5}$ dark, with apical part pale; tibiae pale; tarsi pale with 4th segment dark. Wings hyaline; forewing rounded with speculum closed. Ratios length of M/PM/S: 6.1/1.0/1.0. Propodeum golden-green; anteromedian part with a small semicircular fovea; surface with rather strong to weak sculpture/reticulation; propodeal callus with 3 setae. Petiolar foramen semicircular.

Metasoma: Petiole slightly transverse (as in Fig. 68). Gaster golden-green; oval-shaped in female. Ratio length of mesosoma/length of gaster both sexes = 0.8–0.9.

Distribution.—Canada (Alberta).

Remarks.—This species comes closest to *pubicornis*-group, but differs from the species in this group in the short postmarginal vein and the protruding lateral parts of frons. Therefore I am not prepared to place *cornigera* in this, or any other, group, but regard it as *species sola*.

Chrysocharis sentenaca n. sp.

Type material.—Holotype female labelled "USA: California, San Diego County, Sentenac Canyon, 22.iv.1981, J. Woolley 81/011", in TAMU. Paratypes: 1 female 4 males with same label-data as holotype, 1 female 2 males in coll. LUZM, remaining in TAMU.

Etymology.—Named after place where type specimens were collected, Sentenac Canyon in California.

Diagnosis.—Thoracic dorsum flattened; ocelli small.

Description.—Length of body: Female = 1.1–1.3 mm, male = 0.9 mm.

Head: Entire antenna dark. Apical 2 segments of flagellum fused. HE/MS/MO both sexes: 3.6/1.0/2.2. Malar space 1.5× as wide as width of scape in female and 1.0× in male. Frons metallic purple below suture, metallic greenish-blue above, with strong and small-meshed reticulation. Frontal suture V-shaped. Vertex golden-green, with weak and small-meshed reticulation. Inner orbit of eye with 1 row of setae. POL/OOL/POO: 2.8/1.0/1.3. Occipital margin rounded. Ratio width of head/width of thorax across posterior mesoscutum = 1.2.

Mesosoma: Pronotum without transverse carina. Mesoscutum and scutellum golden-green; with rather strong and small-meshed reticulation on mesoscutum, weaker on scutellum; scutellum about as long as wide. Dorsellum large, 2.9× as wide as long, and almost flat, with weak reticulation. Borderline between lower and upper mesepimeron weakly curved. All coxae dark and metallic with weak reticulation. Femora and tibiae pale; tarsi pale with 4th segment dark; except weakly infuscate fore tibiae and tarsi. Forewing hyaline, rounded with speculum closed, and with a narrow costal cell.

Ratios length of M/PM/S: 4.1/1.8/1.0. Propodeum golden-green; anteromedian part with a small and weak fold; surface with weak reticulation; propodeal callus with 2 setae. Petiolar foramen semicircular.

Metasoma: Petiole very short, in dorsal view visible only as a narrow and smooth strip (as in Fig. 75). Gaster golden-green or golden-purple; oval-shaped in female. Ratio length of mesosoma/length of gaster female = 0.8–0.9, male = 0.9.

Distribution.—USA (California).

Remarks.—*C. sentenaca* belongs to *pen-theus*-group and hence has the characters diagnostic for that group (Hansson 1987: 49) and is similar to *C. submutica*.

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Review of the World Species of *Sigalphus* (Hymenoptera: Braconidae: Sigalphinae) and Biology of *Sigalphus romeroi*, New Species

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Abstract.—Two new species, *Sigalphus romeroi* Sharkey from Costa Rica and *Sigalphus masoni* Sharkey from Nepal, are described. The world species are reviewed, a key to the world species is presented, and the life history of *Sigalphus romeroi* is described.

INTRODUCTION AND HISTORICAL REVIEW

Until recently, there has been little research done on the species of *Sigalphus*. The pre-1973 literature on *Sigalphus* is catalogued in Shenefelt (1973). The more recent literature is summarized here. Tobias (1974) described *Sigalphus mongolicus* from Mongolia. You, Zhou and Tong (1991) described two putative new species of *Sigalphus* from Hunan Province of China, viz. *S. humanus* You and Tong and *S. anomis* You and Tong. Achterberg and Austin (1992) reviewed the world species of *Sigalphus* Latreille and revised the world genera of Sigalphinae. Five species of *Sigalphus* were recognized, viz., *S. bicolor* (Cresson), *S. fulvus* Brues, *S. irrorator* (Fabricius), *S. neavei* (Turner), *S. testaceus* Granger. *S. humanus* and *S. anomis* were synonymized with *S. irrorator*. Achterberg and Austin apparently overlooked *S. mongolicus* Tobias (1974). He and Chen (1993) described two new species from China, *Sigalphus flavistigmus* He and Chen and *Sigalphus nigripes* He and Chen. You and Zhou (1994) revised the Chinese species of *Sigalphus*. They disagreed with Achterberg and Austin's (1992) synonymies and elected to reestablish *S. humanus* and *S. anomis*,

suggesting that these two may represent only one species. He, Chen, and Ma (1994) synonymized *S. anomis* and *S. nigripes* under *S. humanus* and described two new species, i.e., *S. gyrodontus* He and Chen and *S. rufiabdominalis* He and Chen.

In the present paper the world species are reviewed; a key to the world species of *Sigalphus* is presented incorporating two new species, and the life history of *Sigalphus romeroi* n. sp. is described.

Sigalphus can be distinguished from all other genera of Braconidae by the presence of the following combination of characters: metasomal terga 1 to 3 forming a carapace, with a free articulation between metasomal segments 1 and 2 (Fig. 1); hind wing with vein 2CU present and very posterior in position such that the crossvein cu-a is less than $.2 \times$ the length of vein 1CU (Figs 3b).

Although this paper is co-authored, the senior author is the sole authority of the new species of *Sigalphus*, the junior author is responsible for the biological data of *S. romeroi*.

Although widespread, *Sigalphus* has few species; intensive collecting in the New World by members and associates of the Hymenoptera Section of the Canadian Na-

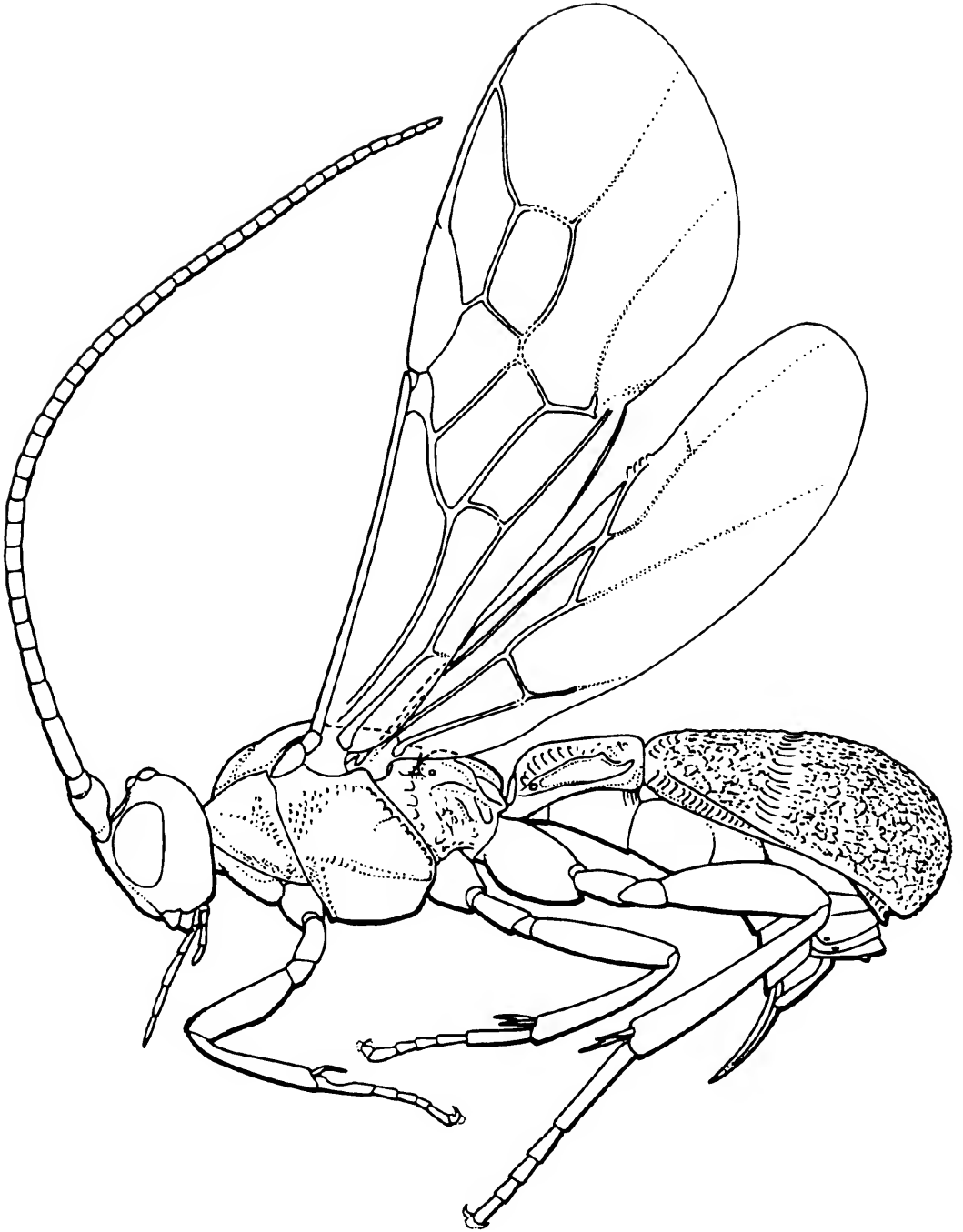


Fig. 1. Lateral aspect of *Sigalphus bicolor*.

tional Collection of Insects, has yielded no new species, and none have been found in the world's major collections. Generally specimens do not appear to be rare, for example *S. bicolor* and *S. irrorator* are well represented in the best North American and European collections. The discovery of a new species in Costa Rica (*S. romeroi*) may be the last such discovery in the New World.

SYNONYMIES

Having seen the type species of both *S. hunanus* You and Tong and *S. anomis* You and Zhou, the senior author agrees with Achterberg and Austin (1992) that they are both junior synonyms of *S. irrorator*. In a recent paper He and Chen (1993) proposed two new species both of which the senior author also considers to be junior synonyms of *S. irrorator*. Although the type specimens have not been made available to the senior author (several requests were made), it is clear from the description that *Sigalphus flavistigmus* He and Chen is a junior synonym of *S. mongolicus*. These two nominal species have similar color patterns except that *S. mongolicus* has the first and second metasomal terga reddish yellow whereas only the second metasomal tergum of *S. flavistigmus* is reddish yellow. Based on color variation in members of *S. bicolor*, of which the senior author has seen a large series of individuals, the color difference between *S. mongolicus* and *S. flavistigmus* is well within the probable range of intraspecific variation. Not only are there no structural characters that sufficiently separate the two species, but the unique specimens of each supposed species were found in close proximity to each other, i.e., north central China and Mongolia, further supporting their conspecific identity. In their recent revision of the Chinese species, He et al. did not consider *S. mongolicus*. It is the senior author's opinion that *S. mongolicus* itself is likely synonymous with *S. irrorator* because they apparently differ only in col-

or characters and trivial morphological characters. This decision will await an examination of the types and a more complete investigation of color variability in *S. irrorator*.

He and Chen (1993) also described *Sigalphus nigripes* which the senior author, in accord with He et al. (1994), considers to be a junior synonym of *S. irrorator*. He and Chen (1993) stated that it is very similar to *S. anomis*, and indeed, it is. The characters of relative lengths of various veins and body parts that were used to separate the two supposed species are insignificant when compared to the intraspecific variation found in both *S. irrorator* and *S. bicolor*. According to He and Chen (1993), one specimen of *S. nigripes* was reared from *Anomis flava* (Noctuidae), the same host species from which the unique specimen of *S. anomis* was reared. This shared host further supports the proposed synonymy of *S. nigripes*. In the most recent of the papers published in China, He et al. (1994) considered *S. nigripes* and *S. anomis* to be junior synonyms of *S. hunanus*.

The senior author is dubious about the specific status of the two new species described by He et al. (1994) as these may also be junior synonyms of *S. irrorator*. Both of these nominative species share with *S. irrorator* (including those entities synonymized with *S. irrorator*) a unique state of sculpture on the second metasomal tergum. This is a central longitudinal groove, which is bordered by two carinae. This groove is divided medially by a weak central keel and the entire depression is areolate-rugose. *S. gyrodontus* and *S. rufiabdominalis* differ from specimens of *S. irrorator* that the senior author has seen in that the two spines at the apex of metasomal tergum 3 are not as sharp as those of *S. irrorator*. The variation in this character in *S. irrorator* does not appear to be great, but series of specimens from the east Palearctic must be checked. These two species are therefore provisionally accepted.

PHYLOGENETIC CONSIDERATIONS

No hypothesis of the phylogenetic relationships of *Sigalphus* species has been published. Achterberg and Austin (1992) analyzed the genera of the Sigalphinae. Despite this valiant first attempt at approximating relationships among the genera, the monophyly of *Sigalphus* is questionable due to the inclusion of the Ethiopian species (*S. fulvus*, *S. testaceus*, and *S. neavei*). Achterberg and Austin (1992) in their cladogram of sigalphine genera cite 4 synapomorphies for the genus; they are all suspect. These will be treated here in the order they appear on the cladogram.

1. "Third tergite with lobes or teeth ventro-posteriorly." This character state is not possessed by any of the three Ethiopian species, conversely it is found in all members of *Aposigalphus* and *Notosigalphus* in a condition almost identical to that of *S. romeroi* (Fig. 2a). Although the character state appears on the cladogram of Achterberg and Austin it is not included in their data set. Species of *Minanga* also have teeth ventro-posteriorly on the third tergum but since these do not emanate from the margin of the tergum as they do in the aforementioned groups their homology is doubtful. The character state has three possible origins given the phylogeny of Achterberg and Austin, viz. a) a synapomorphy for *Sigalphus* + (*Aposigalphus* + *Notosigalphus*) with a loss in the Ethiopian species of *Sigalphus*, b) a synapomorphy for the non-Ethiopian species of *Sigalphus* and a synapomorphy (convergence) for *Aposigalphus* + *Notosigalphus*, or c) a synapomorphy for *Minanga* + (*Sigalphus* + (*Aposigalphus* + *Notosigalphus*)) with a loss in the Ethiopian species of *Sigalphus*. This last hypothesis assumes that the condition in *Minanga* and the other genera is homologous. None of these character state distributions provides support for the concept of *Sigalphus* including the Ethiopian species.

2. "Strongly costate metapleuron." This

is another character that was not included in the Achterberg and Austin data set but rather it was added to the cladogram a posteriori. An assessment of the distribution of this character state shows that the metapleura of the non-Ethiopian species of *Sigalphus* are relatively more costate than those of the Ethiopian species which are mostly rugose, as in species of *Minanga* and *Acampsis*. Again, this character state does not support the monophyly of *Sigalphus*.

3. "First tergite with complete and strong dorsal carina." Although this character state is included in the data matrix, the cladogram does not present the most parsimonious distribution. The data matrix lists the following taxa as possessing the derived character state: *Sigalphus*, *Minanga*, *Acampsis*, and *Afrocampsis*. This distribution is correct, but on the cladogram Achterberg and Austin indicated that the character state is an autapomorphy for *Sigalphus* and ignore the rest of the character state distribution. There are several parsimonious reconstructions of the character but all indicate that the presence of strong dorsal carina on the first tergite is plesiomorphic with reference to *Sigalphus*.

4. "Face with shallow semicircular depression." This depression apparently refers to the two longitudinal depressions that define the raised medial area of the face. Some specimens of *S. irrorator* appear to have these depressions somewhat expanded laterally but in other species of *Sigalphus* there is no discernable difference between these depressions and those of most other genera of Sigalphinae except *Afrocampsis* which does not have them.

In summary, there is no evidence for the monophyly of *Sigalphus* as presently defined. That all four of the putative synapomorphies proposed by Achterberg and Austin are incorrect suggests that their entire analysis is suspect. We do not wish to address generic concepts in this paper, only to draw attention to the fact that care must be taken in interpreting their re-

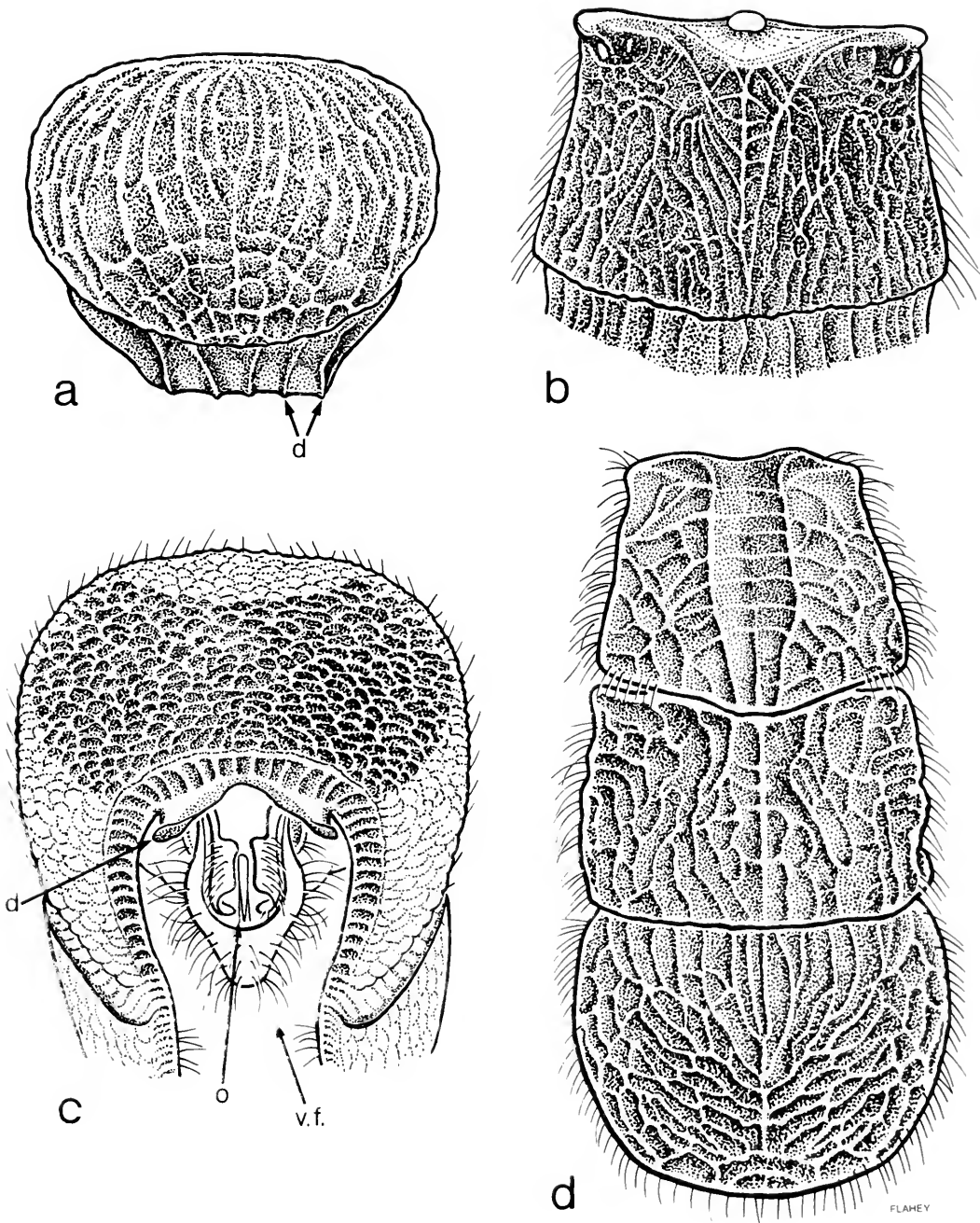


Fig. 2. a, posterior aspect of metasoma of *Sigalplus romeroi* showing ridges on ventral apex (d = denticles); b, dorsal aspect of metasomal tergum 2 of *Sigalplus masoni*; c, posteroventral aspect of metasoma of *Sigalplus masoni* showing denticles at ventral apex (d = denticles, o = ovipositor, v.f. = ventral foramen); d, dorsal aspect of metasoma of *Sigalplus romeroi*.

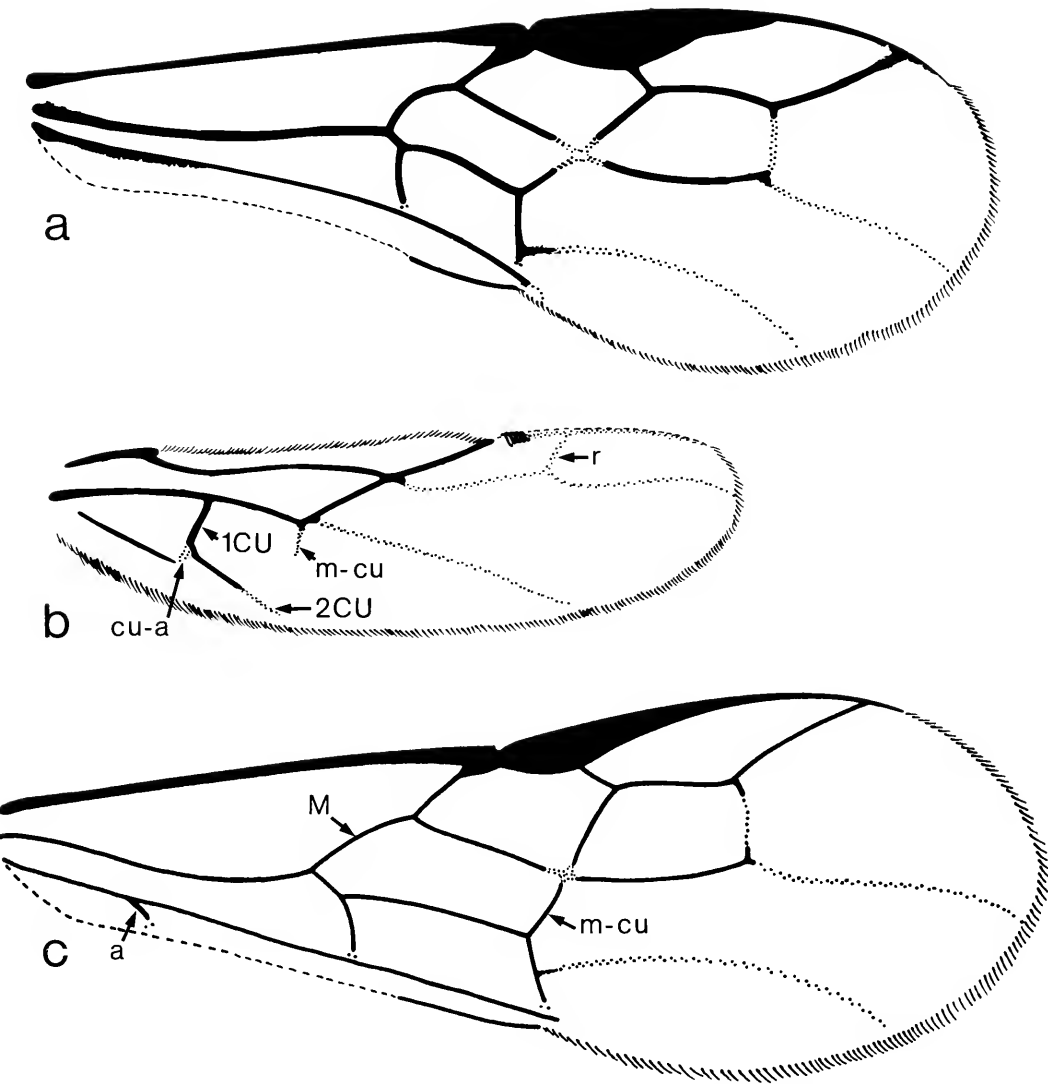


Fig. 3. a, fore wing of *Sigalphus romeroi*; b, hind wing of *Sigalphus romeroi*; c, fore wing of *Sigalphus masoni*.

sults. A phylogenetic analysis of the species of *Sigalphus* must be preceded by a reexamination of the relationships of the genera and this is beyond the scope of this paper. The non-Ethiopian members of *Sigalphus* may be monophyletic, based on the presence of denticles at the ventroposterior margin of tergum 3.

KEY TO WORLD SPECIES OF *SIGALPHUS*

- 1. New World species. 2
- 1'. Old World species. 3
- 2. Metasoma orange; posterior flange of ventral foramen of metasoma smooth apically, ridges reduced to small crenulae not reaching apex of flange (south eastern Canada and eastern U. S. A. south to Florida). *S. bicolor* (Cresson)

| | |
|--|---------------------------------------|
| 2'. Metasoma black; posterior flange of ventral foramen of metasoma with ridges extending to apex (Fig. 2a) (known only from the type locality in northwestern Costa Rica, but the two species of noctuid hosts occur throughout the Mesoamerican Pacific dry deciduous forest and this parasitoid may be found there as well) | <i>S. romeroi</i> n. sp. |
| 3. Head and mesosoma entirely black | 4 |
| 3'. Head and mesosoma not entirely black, rather with pale coloration | 9 |
| 4. Apex of ventral foramen of metasoma lacking denticles and two rounded lobes (southern Africa) | <i>S. neavei</i> (Turner) |
| 4'. Apex of ventral foramen of metasoma with two denticles or two rounded lobes (Fig. 2c) (Oriental, Palaearctic) | 5 |
| 5. Apex of ventral foramen of metasoma with two sharp denticles | 6 |
| 5'. Apex of ventral foramen of metasoma with two rounded lobes | 7 |
| 6. Metasoma entirely black; stigma black (Palaearctic) | <i>S. irrorator</i> (Fabricius) |
| 6'. Metasoma orange and black; stigma yellow (Mongolia and northern China) | <i>S. mongolicus</i> Tobias |
| 7. Tergum 2 with two parallel median longitudinal carinae with a median longitudinal groove between them | 8 |
| 7'. Tergum 2 without two parallel median longitudinal carinae and without a median longitudinal groove | <i>S. masoni</i> n. sp. |
| 8. Fore wing entirely melanic-infusate; tergum 3 as wide as tergum 2 | <i>S. gyrodontus</i> He and Chen |
| 8'. Fore wing melanic-infusate in distal half only; tergum 3 wider than tergum 2 | <i>S. rufiabdominalis</i> He and Chen |
| 9. Vertex of head and apex of hind tibia black (southern Africa) | <i>S. fulvus</i> Brues. |
| 9'. Head and hind tibia entirely reddish brown (Madagascar) | <i>S. testaceus</i> Granger. |

Sigalphus romeroi Sharkey n. sp.
(Figs 2a, d, 3a, b)

MALE.
Length.—8.4 mm.
Color.—Entirely black except fore tarsus brown, wings evenly infusate.
Head.—Antenna with 42–44 flagellomeres.
Mesosoma.—Pronotum smooth except for weak crenulae along posterior border; subpronope present; notaulus deeply impressed and with weak punctures; scutellar furrow (sulcus) smooth except for median longitudinal carina; posterior scutellar depression composed of two large pits; median depression of metanotum semicircular (rounded posteriorly); propodeum entirely areolate, with pair of strong longitudinal carinae defining medial area; sternaulus complete to epicnemial carina; fore wing (Fig. 3a) with veins M and m-cu not distinctly converging anteriorly; crossvein a of fore wing not present; sec-

ondary crossveins r and m-cu of hind wing present though weak and not tubular (Fig. 3b).
Metasoma (Figs 2a, d).—All terga rugose; first tergum with two precurent longitudinal carinae; second tergum with median longitudinal carina, and without deep anterolateral depressions (as in *S. bicolor*); tergum 3 lacking long dense setae; ventral margins of carapace crenulate; apex of ventral metasomal foramen with 6 ridges forming weak, sharp, denticles (Fig. 2a); ventral foramen of carapace not extending to apex of metasoma, i.e., tergum 3 curved around apex of metasoma forming posterior surface.
Material Examined.—Holotype male: COSTA RICA, Guanacaste Province, Guanacaste Conservation Area, Sector Santa Rosa; 300 m. Janzen rearing data base voucher number 90-SRNP-828. Larval host *Epithisanotia sanctijohannasi* (Noctuidae) collected 24 June 1990, wasp

eclosed 26 May 1991. Instituto Nacional de Biodiversidad (INBio), Santo Domingo de Heredia, Costa Rica.

Paratype male: COSTA RICA, Guanacaste Province, Guanacaste Conservation Area, Sector Santa Rosa, 300m. Janzen rearing data base voucher number 92-SRNP-2777. Larval host *Erochia mummia* (species complex) (Noctuidae) collected 7 July 1992, wasp enclosed 10 May 1993. Canadian National Collection, Ottawa, Canada.

Remarks.—The female of this species is unknown. *S. romeroi* is easily distinguished from the only other New World species, *S. bicolor* by the characters given in the key.

Etymology.—The species is named in honor of Sra. Luz Maria Romero in recognition of her outstanding drive and inspiration in guiding and developing the Biological Education Program of the Guanacaste Conservation Area in northwestern Costa Rica.

Biogeographical Notes.—This is the first record of members of the genus *Sigalphus* in the Neotropics and only the second species to be discovered in the New World. The genus is unknown in South America.

As suggested in the section on phylogeny, the non-Ethiopian members of *Sigalphus* may be monophyletic based on the presence of denticles at the ventroposterior margin of tergum 3. If this is so, the distribution of the New World species is interesting from a biogeographic perspective.

It is generally agreed that the closest phylogenetic relationships of most temperate North American taxa are found in the northern hemisphere of the Old World (Lavin and Luckow 1993). In contrast the usual hypothesis put forward to explain North American tropical fauna is dispersal from South America.

If the non-Ethiopian members of *Sigalphus* are monophyletic, it suggests a northern hemisphere origin of *S. romeroi*, the only Neotropical member of the genus. This distribution is consistent with what

has been referred to as the boreotropics hypothesis, which suggests a historically more widespread tropical northern hemisphere biota. (Wolfe 1975; Tiffney 1985a, b; Lavin and Luckow 1993).

Biology.—The larval hosts, *Epithisanotia sanctijohannasi* and *Erochia mummia* (both: Noctuidae, Agaristinae), are common to exceedingly rare (depending on the year) and univoltine in the primary to early successional dry forests in eastern Sector Santa Rosa of the Guanacaste Conservation Area in northwestern Costa Rica (200–300m elevation; about 35 km north of the town of Liberia, to the west of the Interamerican Highway) (see Janzen 1987, 1988a, 1988b, 1993 for a general site description of this forest and its caterpillars). *E. sanctijohannasi* and *E. mummia* are most easily located when they are feeding on the large woody vine *Tetracera volubilis* (Dilleniaceae, Dilleniales) (hundreds of records), and *E. sanctijohannasi* has also been found feeding on *Curatela americana* (4 records). These larvae eat mature leaves and are non-gregarious feeders in the penultimate and ultimate instars (earlier instars unknown) on both host plants. Both species are univoltine (last instar caterpillars occurring in late June and early July, the second and third months of the rainy season) and the pupae remain dormant through the remainder of the six month rainy season and all of the dry season, with the moths eclosing in May at the beginning of the rains (see Janzen 1987, 1988a, 1993 for other examples of the same phenomenon).

Of 36 *E. sanctijohannasi* 31 *E. mummia* last instar larvae collected and reared from *T. volubilis* in 1992 and 1993, 84 and 93 percent respectively produced last instar larvae of *Sigalphus romeroi*. This extremely high percent of parasitization is not representative of caterpillar-parasitoid interactions in this forest, where 1–30% parasitization by a given species of parasitoid is usually recorded (D. H. Janzen, unpublished rearing records). The very large

number of *Sigalphus romeroi* larvae did not generate a large paratype series because, as explained below, the larvae proved to be very incompetent at spinning cocoons and surviving subsequently under artificial rearing conditions.

The parasitized last instar caterpillars of *E. sanctijohannasi* and *E. mummia* appear to be perfectly normal in feeding, fleeing and walking behaviour. The prepupal caterpillar searches in the litter for a piece of rotting wood, tunnels into the wood, and makes its pupal chamber there. Within 1–3 days of the caterpillar entering the wood the wasp larva eats nearly all of the contents of the prepupal caterpillar and exits the cadaver. The wasp larva is so large that there does not appear to be sufficient food for more than one per caterpillar of either host. The wasp larva then spins an ovoid white cocoon in the caterpillar's pupal chamber (late June to early July), where it remains dormant as a prepupal larva until the following May, when it pupates and exits through a round hole cut in the cocoon, and then burrows out through the wood chip-filled entrance tunnel made initially by the caterpillar.

The biology described in the previous paragraphs is based on observation of all of this behaviour with captive caterpillars individually confined in large plastic bags and bottles in an open air laboratory a few meters from the forest where the caterpillars and wasps are found naturally. Dormancy of moth pupae and of wasp larvae in their cocoons occurred in the individuals confined under three conditions of captivity, i.e., under moist conditions throughout the wet season with a change to dry conditions during the dry season, entirely under dry conditions throughout the wet and dry seasons, and for those captured in the dry season they remained in a dry environment in captivity. Moths in the pupal stage and wasp larvae both use some environmental cue that is perceivable through the walls of a plastic bag to initiate further development in late

April or early May, and this cue is most likely the abrupt drop in temperature that accompanies the first rains (see Janzen 1993). By eclosing at the same time as the moths, the adult wasps are presumably present at exactly the same time as are the first instar larvae of the next generation of caterpillars which, extrapolating from the known biology of *S. bicolor*, is the stage most likely to be attacked.

The larva of *Sigalphus romeroi* is exceptional, among the species of parasitoid wasps that the junior author has reared in this forest, in its inability to spin a cocoon except in the pupal chamber of its host. It was usually not able to spin a cocoon between leaves in the litter, among crumpled layers of dry or moist toilet tissue, or in tubular chambers of toilet tissue. Of ten larvae that did succeed in spinning cocoons among toilet tissue layers, all died of unknown causes over the following seven months.

Malaise traps run for the equivalent of tens of years in this dry forest between 1984 and 1988 (e.g., Gauld 1988, Gaston and Gauld 1993) have captured no specimens of *S. romeroi* (I. D. Gauld and P. A. Mitchell, personal communication). This result is particularly striking given that the Malaise traps were located within several meters of the host plants and in all ages of forest succession.

In contrast to *S. romeroi* being large, solitary, and univoltine, *Sigalphus bicolor*, the only North American member of the genus, is small, gregarious and multivoltine. *S. bicolor* oviposits in the first instar larvae of a noctuid caterpillar, *Acronicta clarescens* (= *Apatela clarescens*), and the larvae come out of the prepupal caterpillar and spin their cocoons within the host cocoon (Cushman 1913, who described the wasp's natural history under the name *Sphaeropyx bicolor*). The only western Palearctic species of the genus, *S. irrorator* has also been reared from *Acronicta* in Europe, but because of its large size (about the same as *S. romeroi*) it is inferred to be solitary (*S.*

Ward, personal communication). You, Zhou and Tong (1991) report *S. irrorator* (as *S. anomis*) as a parasitoid of *Anomis flava* (Noctuidae). The biology of all other species of *Sigalphus* is unknown.

Sigalphus masoni Sharkey n. sp.
(Figs. 2b, c, 3c)

HOLOTYPE FEMALE.

Length.—10.9 mm.

Color.—Mostly black with yellow on bases and ventral sides of all tibiae and on metasomal sterna, and orange on metasomal terga 1, 2, and anterior $\frac{2}{3}$ of tergum 3; fore wing entirely infusate though somewhat paler basally; hind wing clear in basal $\frac{1}{3}$, infusate in distal $\frac{2}{3}$.

Head.—Antenna broken.

Mesosoma.—Pronotum weakly rugose; subpronope present; notaulus deeply impressed and crenulate; scutellar furrow (sulcus) smooth except for three longitudinal carinae; posterior scutellar depression composed of many small pits; median depression of metanotum sharply triangular (acute posteriorly); propodeum weakly rugose laterally with pair of longitudinal carinae defining medial area; sternaulus complete to epicnemial carina; fore wing with veins M and m-cu distinctly converging anteriorly; crossvein a of fore wing present and distinct; hind wing with secondary crossvein r present and secondary crossvein m-cu absent.

Metasoma (Figs 2b, c).—All terga rugose; first tergum with two precurent longitudinal carinae; second tergum with median longitudinal carina and an equally strong pair of lateral longitudinal carinae that converge towards the mid-line posteriorly; second tergum with moderately deep anterolateral depressions (as in *S. bicolor*); tergum 3 with long dense setae; ventral margins of carapace crenulate; apex of ventral metasomal foramen with two rounded denticles (Fig. 2c); ventral foramen of carapace (Fig. 2c) not extending to apex of metasoma.

Material Examined.—Holotype ♀: NE-

PAL: Katmandu, Godavari, 5,000 ft. (1524 m.), 6.VIII.1967, Canadian Nepal Expedition, [Canadian National Collection, Ottawa, Canada]

Biology.—Unknown

Remarks.—Members of *S. masoni* are similar to those of *S. irrorator* and *S. mongolicus* in some respects, particularly in their general size and the long setae on metasomal tergum 3. In *S. masoni*, these setae are longer and denser than in the New World species of *Sigalphus*, though they are not as exaggerated as those of *S. irrorator*, nor are they gold colored. Members of the two species differ in color, those of *S. masoni* having the metasoma predominantly orange versus entirely black in *S. irrorator*. The species also differ in the shape of the denticles at the apex of the ventral foramen, i.e., those of *S. masoni* are wide and blunt whereas those of *S. irrorator* and *S. mongolicus* are relatively narrow and acute. The most distinctive feature distinguishing *S. masoni* from other species of *Sigalphus* is the sculpture of the second metasomal tergum. All other Palearctic and Oriental species of *Sigalphus* have a median longitudinal groove bordered laterally by longitudinal carinae. These are not present in *S. masoni* (Fig. 2d).

Etymology.—The species is named after Dr. W. R. M. Mason for his many contributions to Hymenopterology, and also, though it is not stated on the label, because he is thought to be the collector of the unique specimen.

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Jason Hardis drew the fore wing *S. masoni*. All other drawings were done by Barry Flahey. We thank David Althoff, Paul Marsh, Lubomir Masner, Eric Rick-ey, Ales Smetana and two anonymous reviewers for valuable comments on early drafts.

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Ovipositor Steering Mechanisms in Braconid Wasps

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Abstract.—Ovipositor features which allow the ovipositor tip to be manipulated and which have restricted distributions among the subfamilies of Braconidae are described and illustrated for the first time. Members of the Amicrocentrinae, Charmontinae, Helconinae and Macrocentrinae have the rhachis (the tongue-like part of the mechanism that interlocks the upper valve with the lower ones) with an increased density of scale-like sculpture and often also swollen pre-apically. This modification leads to increased friction and restricted movement between the upper and lower valves and is also associated with an ovipositor bending mechanism in which retraction of the lower ovipositor valves relative to the upper one causes the ovipositor tip to bend ventrally. Many members of the subfamilies Agathidinae and Orgilinae possess a pair of pre-apical boss-like projections on the upper ovipositor valve (gonapophyses 9) and a corresponding structure on each lower valve (gonapophyses 8) that together enable the wasps to bend and manipulate the ovipositor apex by retraction of the lower ovipositor valves relative to the upper one. Most members of the Doryctinae have the aulax (the groove-like part of the mechanism that interlocks the lower valve with the upper one) constricted opposite modified pre-apical, dorso-lateral tooth-like structures. These constrictions restrict the relative movement between the upper and lower valves and thus operate as an ovipositor bending mechanism. The potential phylogenetic significance of these mechanisms is discussed, and preliminary parsimony analyses are described which suggest that the pre-apical boss-like projections of the Agathidinae and Orgilinae may represent a synapomorphy uniting these two subfamilies.

INTRODUCTION

Oviposition behaviour and, as a consequence, the ovipositor have been of immense importance in the evolution of the Hymenoptera, and are central to the parasitic way of life (Gauld & Bolton 1988). The commonly held view that the ovipositors of parasitic wasps are fairly simple analogues of hypodermic needles is therefore likely to be a considerable over-simplification as has in fact been shown by several previous investigations of functional morphology (Oeser 1961; Austin & Browning 1981; Quicke et al. 1992a,b, 1994).

Several braconid genera have recently been shown to possess highly modified

ovipositors whose tips are capable of being independently actively manipulated by the wasp even though the ovipositor valves themselves are devoid of intrinsic musculature and their relative movements are controlled by muscles within the metasoma. Mechanisms, as found for example in the braconine genus *Zaglyptogastra* Ashmead, were apparent because of very conspicuous features of the intact ovipositor (Quicke 1991; Quicke & Marsh 1992). However, an ability to manipulate or steer the ovipositor tip has been observed in a number of other parasitic Hymenoptera whose ovipositors appear more or less unmodified externally (Delanoue & Arambourg 1965; Compton & Nefdt 1988). Further, our own observations have also

shown that an ability to manipulate the ovipositor tip is present in members of several subfamilies of Braconidae that possess moderately long ovipositors. We have therefore examined ovipositor tip structure in detail across a range of braconid taxa. Here we describe three different types of morphological specialisation found in the Braconidae that appear to underlie the manipulatory abilities observed. These modifications all utilise the same mechanical principle but they achieve this through modification of different structures. In these cases, the structures involved can often only be revealed by examination of separated ovipositor valves using scanning electron microscopy; however, their existence supports the view that the ovipositors of parasitic wasps are highly specialised and complex structures.

Two different ovipositor steering mechanisms, one involving a sinuous apical region of the ovipositor the other involving the development of an aulaciform rod between the largely separated halves of the upper ovipositor valve have been reported previously (Quicke 1991; Quicke et al. 1994). The first of these is possessed by several unrelated taxa of Braconidae and Ichneumonidae, the second so far is known only from members of the Ichneumonidae. During investigations of ovipositors belonging to a large number of other ichneumonid wasps collectively representing most subfamilies, no steering specialisations similar to any of the three described here for Braconidae have been detected. Functionally similar but morphologically different mechanisms in members of two other families of parasitic Hymenoptera, Gasteruptiidae and Aulacidae, are being described elsewhere (Quicke & Fitton, in press).

GENERAL MORPHOLOGY

The ovipositors of Hymenoptera are comprised of components that are believed to be derived primitively from two pairs of metasomal appendages (Smith

1968, 1970). The two gonapophyses of abdominal segment 9 are usually fused along their length and form the single upper valve, while those of segment 8 remain separate and form the two lower valves. The upper valve is interlocked with each lower valve by a longitudinal tongue and groove joint referred to as the olistheter. The tongue or rhachis situated ventro-laterally on each side of the upper valve is 'T'-shaped in transverse section and in life runs within the 'T'-shaped groove or aulax on the dorso-lateral face of the lower valve (Fig. 1).

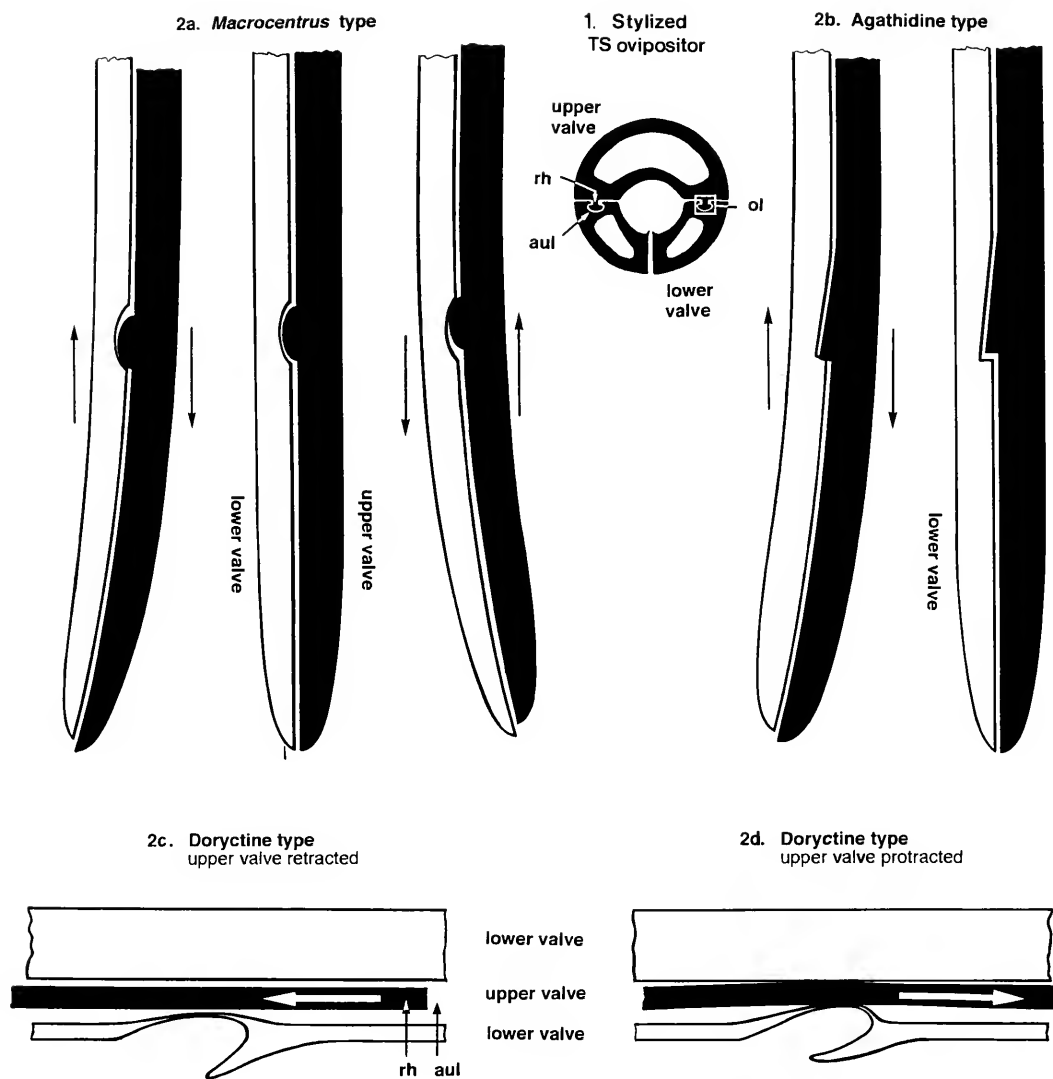
MATERIALS AND METHODS

Ovipositors of 70 species of Braconidae, collectively representing members of 19 of the 40-or-so currently recognised subfamilies (Quicke & van Achterberg 1990; Shaw & Huddleston 1991) have been examined using scanning electron microscopy. For most of these, the upper and lower valves were carefully separated after soaking intact wasp metasomas or excised ovipositors in either water or dilute aqueous mild detergent. In the case of a few specimens in which one or both lower ovipositor valves were protruding beyond the apex of the dorsal valve, the intact ovipositor was examined.

Limited observations of ovipositor manipulation were made on some hand-held living female wasps. In addition, experiments were carried out using excised ovipositors from freshly killed wasps. Ovipositors were submerged under water and the effects observed of pulling and pushing the cut ends of the basal portions of the upper and lower valves differentially with fine forceps.

The taxa investigated are listed below according to subfamily. Where more than one individual of a species was examined the number is given in parentheses.

Agathidinae: *Braunsia* sp., Cameroun (3); *Camptothlipsis* sp., Kenya; *Megagathis* sp., Sierra Leone; *Microdus rufipes* Nees, UK. Alysiinae: *Phaenocarpa conspurcator*



Figs. 1, 2. 1. Diagrammatic transverse section (TS) through mid-region of braconid ovipositor to show olistheter mechanism: (ol) olistheter, (rh) rhachis, (aul) aulax. 2. Diagrammatic representations of how the three ovipositor bending mechanisms are believed to operate. a, Macrocentrinae, Amicrocentrinae, and Charmontinae, lateral views showing preapical swelling of rhachis; b, Agathidinae and Orgilinae, lateral views showing pre-apical bosses; c, d, Doryctinae, dorsal showing in the postulated increased grip against the rhachis when the upper valve is protracted.

(Haliday), Netherlands. Amicrocentrinae: *Amicrocentrum* sp., Tanzania. Blacinae: *Artiocus spinarius* Achterberg, Brazil (2); *Blacus hastatus* Haliday, Sweden; *B. longipennis* (Gravenhorst), UK; *B. maculipes* Wesmael, Austria; *B. nigricornis* Haeselbarth, UK; *B. paganus* Haliday, UK; *B. pallipes* Haliday, UK; *B. ruficornis* Nees, Hungary,

Russia (2); *Dyscoletes lancifer* (Haliday), UK, Germany (2). Braconinae: *Digonogastrea* sp., Trinidad; *Euurobracon yokahamae* Dalla Torre, Japan; *Glyptomorpha* sp., Gambia; *Nesaulax* sp., Papua New Guinea; *Odesia* sp., Kenya; *Virgulibracon endoxylaphagus* Quicke & Ingram, Australia. Cardiochilinae: *Cardiochiles* sp., Cameroun. Cen-

ocoeliinae: *Capitoniuss* spp., Brazil (2). Charmontinae: *Charmon cruentatus* Haliday, UK (2). Doryctinae: *Acanthodoryctes tomentosa* (Szépligeti), Australia; *Acrophasmus ferrugineus* (Marsh), USA; *Allorhogas pyralophagus* Marsh, Trinidad; *Binarea* sp., Argentina; *Doryctes erythromeles* (Brullé), USA; *Liobracon* sp., Brazil; *Megaloproctus platyantennus* Marsh, Brazil; *Monarea* sp., Brazil; *Rhaconotus* sp., USA; *Rutheia* sp., Bolivia; *Syngaster* sp., Australia; *Spathius* sp., Kenya; *Zombrus* sp., Kenya. Helconinae: *Austrohelcon* sp., Australia; *Aspicolpus carinator* Nees, Hungary; *Aspidocolpus* sp., Nigeria; *Baesis abietis* (Ratzeburg), Poland; *Brulleia latiannulatus* (Cameron), New Guinea; *Calohelcon obscuripennis* Turner, Australia; *Diospilus capito* (Nees), Hungary (2); *Diospilus morosus* Reinhard, Austria; *Eubazus pallipes* Nees, Romania; *E. tibialis* Haliday, Bulgaria; *E. (Brachistes)* spp., Argentina, UK (2); *Helcon nunciator* Fabricius, Hungary; *Helconidea tentator* (Fabricius), Belgium; *Polydegmon sinuatus* Foerster, Hungary; *Taphaeus hiator* Thunberg, Hungary; *Wroughtonia* sp., Canada; undescribed genus A, Australia; undescribed genus B, Australia. Homolobinae: *Homolobus truncator* (Say), Bulgaria (2); *H. (Oulophus)* sp., USA. Macrocentrinae: *Austrozele uniformis* Provancher, USA; *Macrocentrus linearis* Nees, Hungary (2); *Macrocentrus* sp., Poland. Microgastrinae: *Sathion falcatus* (Nees), Germany. Microtypinae: *Microtypus* sp., Hungary. Opiinae: *Doryctobracon* sp., Trinidad. Orgilinae: *Orgilus leptcephalus* (Hartig), Germany; *Orgilus* spp., Cameroun, France (3); *Orgilonia* sp., Cameroun; *Stantonia* sp., Cameroun. Pambolinae: *Monitoriella elongata* Hedqvist, USA. Pselaphaninae: *Pselaphanus trogoides* Szépligeti, Surinam. Rhysipolinae: *Rhysipolis* sp., UK

RESULTS

Upper Valve Rhachis Scaling and Expansions

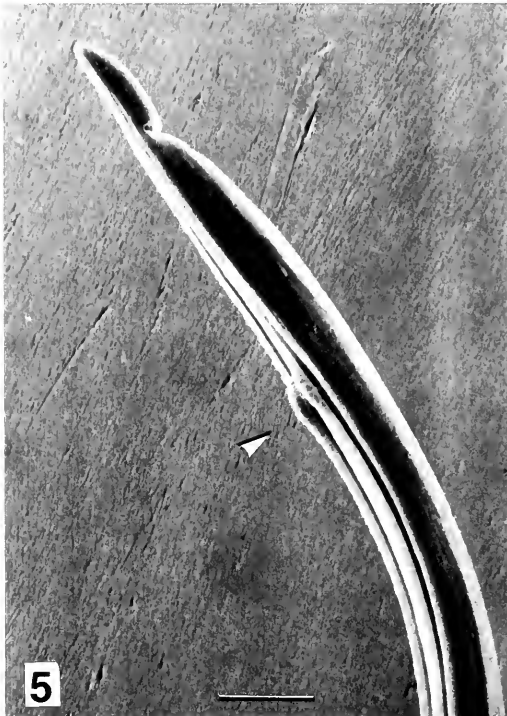
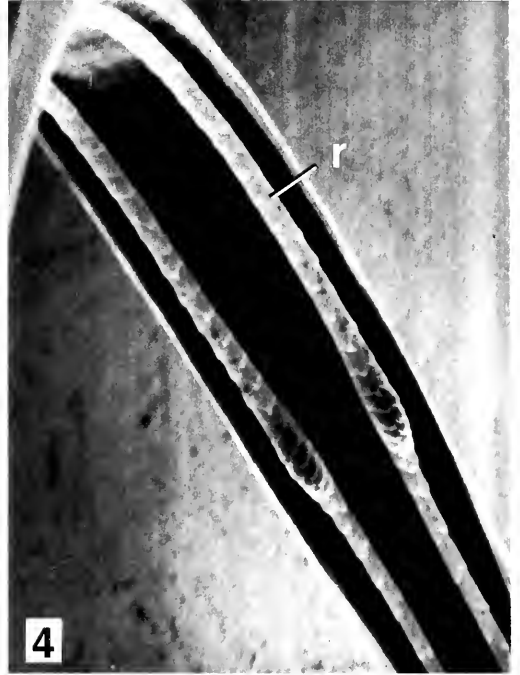
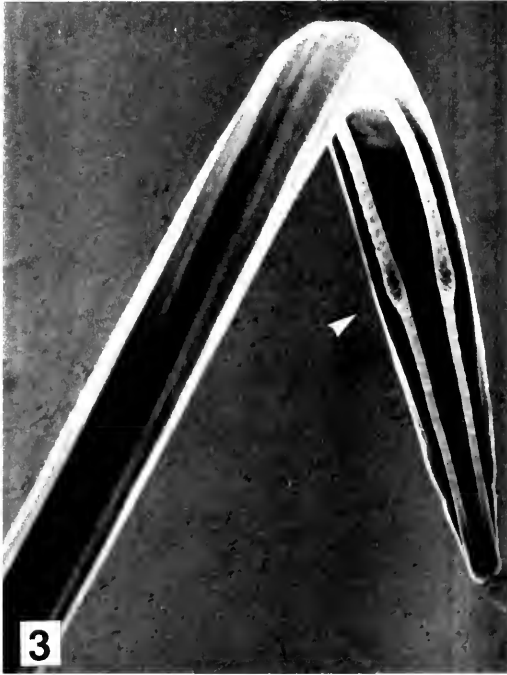
In all Hymenoptera both the rhachis and the margins of the aulax are furnished

with scale-like sculpture which, in the case of the parasitic Apocrita and the Orussidae, are generally rather widely spaced (Figs. 16, 17). In the Amicrocentrinae, Blacinae, Charmontinae and Helconinae the density of scaling was found to be considerably increased over a short region preapically (Figs. 3–11). Further, in the Charmontinae and Macrocentrinae this is accompanied by a distinct swelling of the rhachis (Figs. 3–6; arrowed) and slight widening of the corresponding length of the aulax.

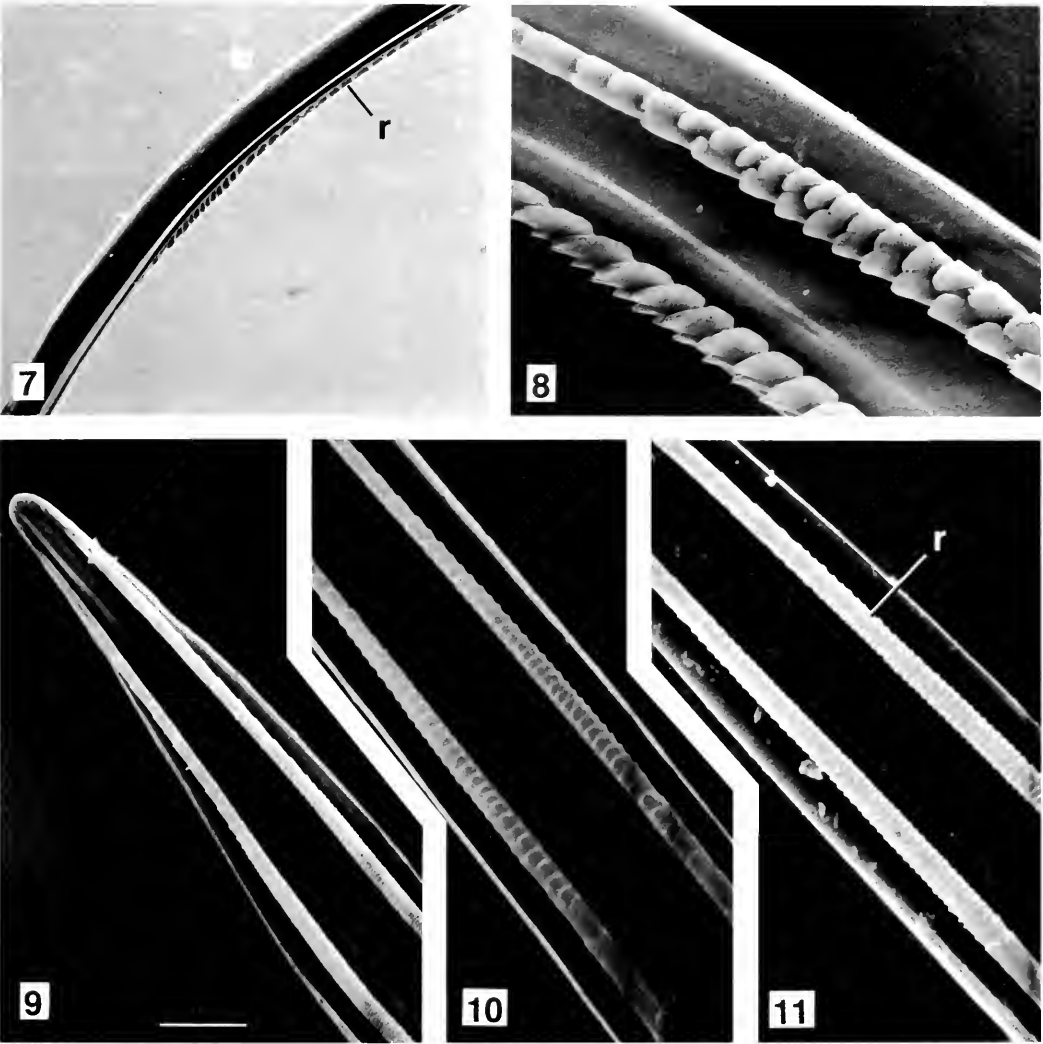
Observation of living *Macrocentrus* females held in the hand showed that they are capable of bending the apex of their ovipositors ventrally through nearly 90°. It seems likely that this is achieved in an analogous way to that proposed for the Agathidinae and Orgilinae (see below), with the swollen and more coarsely sculptured region of the rhachis providing increased resistance to relative movement of the ovipositor valves at the apical part of the ovipositor. Thus, if the dorsal valve is protracted relative to the ventral ones, they will not be able to slide past one another freely at the apex, and so the ovipositor will be forced to curve ventrally in order to accommodate the relative extension of the upper valve in a manner analogous to the bending of a bimetal strip in a thermostat, as illustrated diagrammatically in Fig. 2a. The plausibility of this was conclusion was substantiated by manipulation of the cut ends of an excised *Macrocentrus* ovipositor which showed that protraction of the upper valve relative to the lower one causes a ventral curving of the ovipositor tip.

Upper and Lower Valve Bosses

In all members of the Orgilinae and most Agathidinae examined, the pre-apical lateral margins of both the upper (Figs. 12, 13, 16, 17) and lower (Figs. 14, 15) ovipositor valves possess an abrupt escarpment-like boss in lateral aspect. These structures are located lateral to the olis-



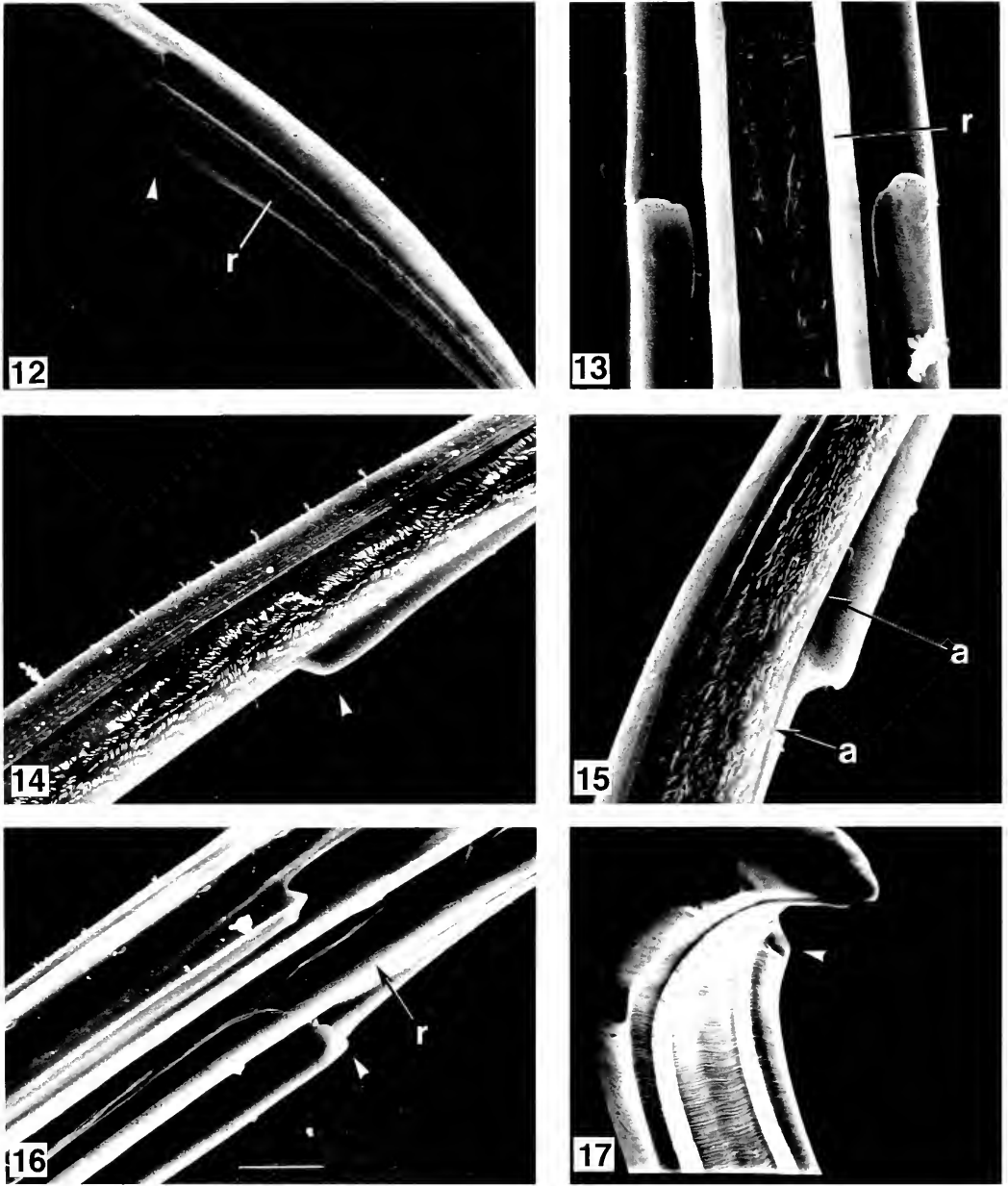
Figs. 3–6. Scanning electron micrographs of apical parts of isolated upper ovipositor valves showing preapical expansion of rhachis (r) with denser scaling (arrows). 3, 4 (detail), *Charnon cruentatus*. 5, *Macrocentrus linearis*. 6, *Macrocentrus* sp. Scale line: 3, 5: 50 μ m; 4, 6: 25 μ m.



Figs. 7–11. Scanning electron micrographs of apical parts of isolated upper ovipositor valves showing weak preapical expansion of rhachis (r) with denser scaling (arrows). 7, 8, *Amicrocentrum* sp. 9, *Helconidea tentator*. 10, *Wroughtonia* sp. 11, *Brulleia latiammulatus*. Scale line: 7: 100µm; 8: 20µm; 9, 50µm; 10, 11: 40µm.

theter. In the case of the dorsal valve, the steep (scarp) face of the stop is at the distal end of the modified region whereas it is at the proximal end in the lower valve. The positioning of these modifications is such that when the ovipositor is in its resting position with neither upper nor lower valves apically protruding beyond the other, the scarp faces of both processes are closely apposed. The presence of these stops limits the relative longitudinal

movement of the upper and lower valves such that the upper valve cannot be protracted apically, relative to the lower valves, beyond the resting position though the upper valve can be retracted basally. The functional significance of this modification was revealed when living agathidines of the genus *Agathis* were held in the hand and the apical part of the ovipositor was observed to change its degree of ventral curvature as the wasp attempted to



Figs. 12-17. Scanning electron micrographs of apical parts of isolated upper (12, 13, 16, 17) and lower ovipositor valves (14, 15) showing (arrows) corresponding preapical, bosses lateral to the rhachis (r) and aulax (a) of the upper and lower valves respectively. 12, 13, 15, *Braunsia* sp. 14, 16, *Megagathis* sp. 17, *Orgilonia* sp. Scale line: 12: 50 μ m; 13, 16: 20 μ m; 14, 15: 30 μ m; 17: 35 μ m.

free itself. Such bending appeared to be achieved by the wasp protracting the upper valve posteriorly relative to the lower valves, thereby forcing together the op-

posing scarp faces of their bosses. Because the valves are interlocked along their whole length by the olistheter mechanism, the ovipositor is forced to curve ventrally,

as illustrated in Figure 2b. The plausibility of this conclusion was substantiated by manipulation of the cut ends of an excised *Agathis* ovipositor which showed that protraction of the upper valve relative to the lower one causes a ventral curving of the ovipositor tip.

No other braconids examined possessed this modification and since neither the Agathidinae nor the Orgilinae are likely to be the most basal of extant braconids (Quicke & van Achterberg 1990; Wharton et al. 1992; van Achterberg & Quicke 1992) (for example, because of their koinobiont endoparasitoid life history), it seems likely that the presence of a scarp-like stop mechanism is apomorphic. The potential implications of this are dealt with in the discussion.

Pre-apical Constrictions of the Aulax

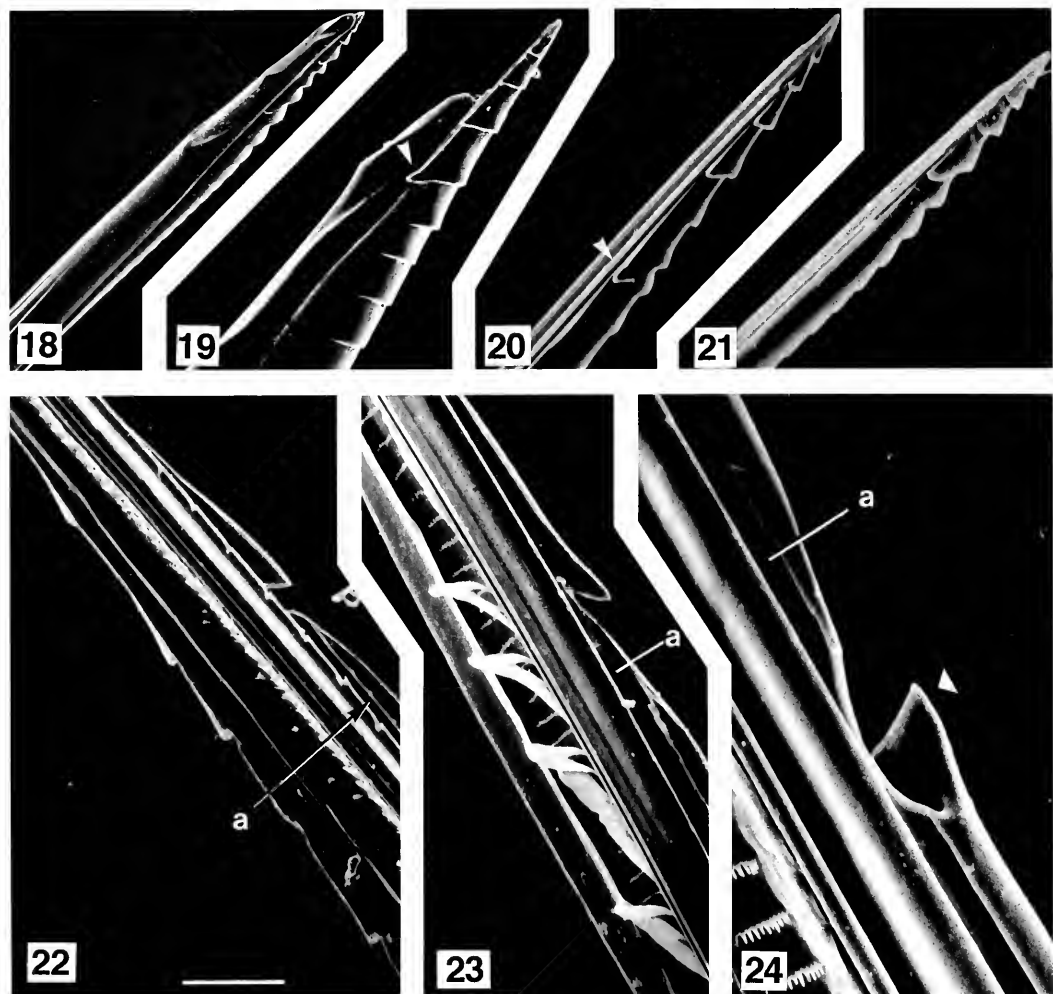
Unlike other braconid subfamilies, most members of the subfamily Doryctinae have the apex of the ovipositor much darker (piceous or black) and much more strongly sclerotized than the remainder (Quicke et al. 1992a) such that it is usually extremely difficult to separate the valves for study even after softening in aqueous potassium hydroxide; though with persistent manipulation, the three parts could usually be separated. Scanning electron microscopy shows that in many genera (e.g. *Binarea*, *Liobracon*, *Monarea*, *Syngaster*, *Zombrus*) the apical part of the lower valves, as well as having ventro-lateral serrations, also possess one or two apparently distinct dorso-lateral tooth-like structures (Figs. 18–21; arrows) (Quicke et al. 1992a). The significance of these in terms of ovipositor steering has been revealed by examination of the adjacent part of the aulax. The aulax is an approximately parallel-sided groove along most of its length, in isolated ventral valves it is strongly constricted opposite these additional teeth by an infolding of the lateral margin (Figs. 22–24). Together with the increased sclerotization of the ovipositor tip

and our observation that it is very difficult to separate the dorsal and ventral valves at the tip region, we conclude that the narrowed region of the aulax acts to grip the rhachis tightly, thereby reducing the freedom of movement of the valves near to the ovipositor tip. The asymmetric arrangement of the constrictions of the aulax are such that retraction of the upper valves is likely to afford less resistance than protraction (Figs. 2c cf d) which will cause the lateral wall of the aulax to roll inwards thus increasing the friction against the rhachis. This prediction was borne out by observations of living *Hecabolus* females which were found to be able to bend their ovipositors ventrally but not dorsally.

DISCUSSION

In all the cases in which we have found to possess probable ovipositor steering mechanisms, their hosts are concealed insect larvae. Orgilines mostly attack weakly concealed hosts such as leaf miners, and they probe into their hosts' tunnels often through frass holes rather than by boring directly through the plant material (Flanders & Oatman 1982; Shaw & Huddleston 1991). Agathidines, charmontines and macrocentrines similarly attack weakly concealed hosts such as leaf rollers, leaf tiers, shoot borers, and, particularly in the case of the Agathidinae, leaf miners/tunnellers. The steering mechanisms may therefore enable the wasps to locate their hosts better within their concealed feeding places. It may also enable the wasps to place their eggs accurately on or within their hosts. In the case of agathidines, for example, it is known that eggs are usually placed very precisely within or next to the host's central nervous system (references in Shaw & Huddleston 1991). Given that their hosts are concealed and often relatively small, such accurate egg placement would be facilitated by the existence of some sort of directional control of the ovipositor tip.

In contrast to the above mentioned sub-



Figs. 18–24. Scanning electron micrographs of apical parts of intact ovipositors (18, 19) and isolated lower ovipositor valves (20–24) of doryctine braconids showing dorso-lateral tooth like structures (arrow) and in 24, the corresponding narrowing of the aulax (a). 18, *Megaloproctus platyantennus*. 19, 24, *Binarea* sp. 20, *Acrophasmus ferrugineus*. 21, *Spathius* sp. 22, *Syngaster* sp. 23, *Zombrus* sp. Scale line: 18: 130 μ m; 19: 70 μ m; 20, 21: 60 μ m; 22, 23: 30 μ m; 24: 10 μ m.

families, many members of the Doryctinae attack more strongly concealed insects such as wood-boring beetle larvae, and since they are idiobiont ectoparasitoids, the exact placement of the paralysing sting or of the egg is usually likely to be of little importance. The process of boring through bark or other hard substrates may not be very accurate and is also quite time consuming, which in turn probably places the wasp under an increased risk of pre-

dation. Locating a host tunnel might therefore be a good first step towards reaching a host if the wasp can subsequently manipulate its ovipositor tip. Steering mechanisms might be seen in these cases as an adaptation which overcomes some of the potential problems of reaching a concealed host directly through a thick layer of substrate.

Of some surprise was that we failed to find any morphological modifications that

could be involved in ovipositor steering in a number of taxa with long to very long ovipositors such as members of the braconine genera *Archibracon*, *Euurobracon*, *Glyptomorpha*, *Nesaulax*, *Odesia* and *Virgulibracon*. Nor were any steering mechanisms identified in the Alysiniinae, Cardiochilinae, or Cenocoeliinae examined. Observations of living females of these taxa would be valuable as it is quite possible that they have some other, perhaps less conspicuous, mechanisms that enable them to manipulate their ovipositors or ovipositor tips. Certainly for many of the braconines with long ovipositors, oviposition involves boring through hard wood (van Achterberg 1986) and this may pose limitations on the bending mechanisms they might possess. Alternatively, it may be that most braconines that attack deeply concealed, wood-boring hosts are simply not adapted to hit the host's tunnel first and then to use the ovipositor to follow the tunnel to the host, but rather reach their hosts by drilling directly through the substrate to them. If this is generally the case, then the strong, possibly defensive, smell of most braconines (Quicke 1988; Quicke & Wharton in preparation) could be an adaptation to protect them during protracted periods of drilling for hosts, during which time they may be particularly vulnerable to predation.

Interestingly, the Agathidinae and Orgilinae did not appear together in the phylogenetic analyses of Quicke & van Achterberg (1990) and Wharton et al. (1992) though their relationships were rather labile. These two subfamilies have a similar general appearance and perhaps more importantly, have two other putative synapomorphies, a relatively narrow forewing marginal cell with an approximately straight vein 3-SR, and in those species with a complete 2nd submarginal cell, this is small and usually triangular or at least has vein 2-SR very short. The discovery of a new apomorphous character present in both, further suggests the possibility that

they could be sister groups, though the possibility also exists that the ovipositor bending mechanisms possessed by members of the two subfamilies reflect convergence as a result of the similarities in their hosts' biologies. In a preliminary investigation, we have added the presence or absence of an ovipositor boss as an additional character to a data matrix of braconid subfamilies based on that of Quicke & van Achterberg (1990) modified in accordance with the suggestions of Wharton et al. (1992) and of van Achterberg & Quicke (1992). Whereas the Agathidinae and Orgilinae did not appear as sister groups in the most parsimonious trees (length 391), trees with them so arranged were only one step longer than the most parsimonious ones obtained. The absence of this character in the Pselaphaninae might be taken to indicate that they are not the sister group of the Agathidinae (van Achterberg 1985), however, it should be noted that in *Pselaphanus*, the ovipositor is rather robust and is probably unsuited to "steering" and that such a mechanism could have been secondarily lost. In this context, it should also be noted that members of some genera of Agathidinae that have shorter and more robust ovipositors were also found to lack the bosses, and therefore this feature may be readily lost in species whose ovipositors evolve to become less flexible. We therefore conducted a second phylogenetic analysis on the data matrix described above but this time scoring the Pselaphaninae as unknown for the new ovipositor character, thus allowing the possibility of a reversal in that group without adding to tree length. In this case the most parsimonious trees included a subset containing the clade (Orgilinae + (Agathidinae + Pselaphaninae)). We therefore suggest that the newly discovered ovipositor features should be incorporated in future phylogenetic analyses of the Braconidae.

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The Wasp Genus *Tachytella* Brauns, 1906 (Hymenoptera: Sphecidae)

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Abstract.—The southern African genus *Tachytella* Brauns includes *aureopilosa* Brauns, 1906 (western South Africa) as well as two new species: *heliophila* (western Namibia) and *nana* (southern Namibia, northwestern South Africa). A lectotype is designated for *Tachytella aureopilosa* var. *nana* Arnold, 1936, the latter name being synonymized with *Tachytella aureopilosa* Brauns, 1906. The genus is redescribed using previously known and newly discovered characters, a key to the species is provided, and phylogenetic relationships between the species are discussed.

INTRODUCTION

General.—*Tachytella* Brauns, a little known genus from southern Africa, was thought to be monotypic until now. Specimens are rarely collected (Bohart and Menke 1976, for example, knew of only six). A decade ago, I discovered an undescribed species in materials from the State Museum Windhoek that Ole Lomholdt, then at the Zoological Museum, Copenhagen, kindly had transshipped to me. During our expedition to Namibia in 1990, Maximilian Schwarz and I collected specimens that represented another new species. These findings prompted me to revise the genus. I follow the format used for my revisions of *Kohliella* Brauns, *Holotachysphex* de Beaumont, and *Gastrosericus* Spinola (Pulawski 1991, 1992, 1995).

Technical Terms.—Most morphological terms follow Bohart and Menke (1976), but the mandibular terms are taken from Michener and Fraser (1978). The following terms are here redefined for convenience:

Clypeal lobe: the projecting medioventral portion of the clypeus.

Mandible:

—**adductor ridge:** extends distad from the adductor swellings (on the inner side) and gradually becomes visible from the outside, constituting the distal part of

the mandibular posterior margin; the two portions differ in size, the distal one being higher than the basal one;

—**condylar ridge:** arises from the condyle, extends distad, and forms the basal portion of the posterior mandibular margin; it is angulate distally in many *Larriinae*;

—**condyle:** mandibular articulation on the occipital side of the head capsule;

—**notch:** an emargination on the posterior margin, delimited basally by the condylar ridge and distally by the expanded portion of the adductor ridge;

—**posterior margin:** extends between the condyle and mandibular apex; called externoventral margin by Bohart and Menke (1976) and lower margin by Michener and Fraser (1978); it actually consists of two components: the condylar ridge basally and the adductor ridge distally (the term *posterior* is preferred because the head is hypognathous, and this edge is thus oriented posterad);

Sternum, tergum: shortened terms for gastral sternum, gastral tergum.

Vertex:

—**length:** the distance between a hind-ocellus and an imaginary line connecting eye hindcorners (i.e., the point where the

inner and the posterior portions of the orbit meet);

—**width**: the shortest interocular distance in the ocellar region.

Origin of Material.—The 29 specimens examined apparently are all that have been collected so far. Institutional or personal collections in which the material is deposited are abbreviated in the text as follows (names of contact persons are given in parentheses):

- AMG: Albany Museum, Grahamstown, South Africa (Friedrich W. Gess).
- BMNH: British Museum (Natural History), London, current nonstatutory name: The Natural History Museum (Lorraine Ficken).
- CAS: California Academy of Sciences, San Francisco, California (Wojciech J. Pulawski).
- FSCA: Florida State Collection of Arthropods, Gainesville, Florida (Lionel A. Stange, James R. Wiley).
- MS: Maximilian Schwarz, Ansfelden bei Linz, Austria (personal collection).
- SAM: South African Museum, Cape Town, South Africa, including G. Arnold collection previously housed in Bulawayo, Zimbabwe (Margie A. Cochrane, Vincent B. Whitehead).
- TMP: Transvaal Museum, Pretoria, South Africa (Iléma Fourie).
- USNM: Smithsonian Institution, National Museum of Natural History, Washington, D.C. (Arnold S. Menke).

Genus *Tachytella*

Tachytella Brauns, 1906:56. Type species: *Tachytella aureopilosa* Brauns, 1906, by monotypy.

Diagnosis.—*Tachytella* is a member of Larrini (Bohart and Menke 1976) and thus has the hindocelli modified to flat, elon-

gate scars (Figs. 8, 12, 20), the only remnant of a lens being a narrow, translucent band along the scar's outer margin (the band is broadly interrupted on the scar's posterolateral or lateral side, depending on its orientation). Within the tribe, *Tachytella* can be recognized by the following four characters:

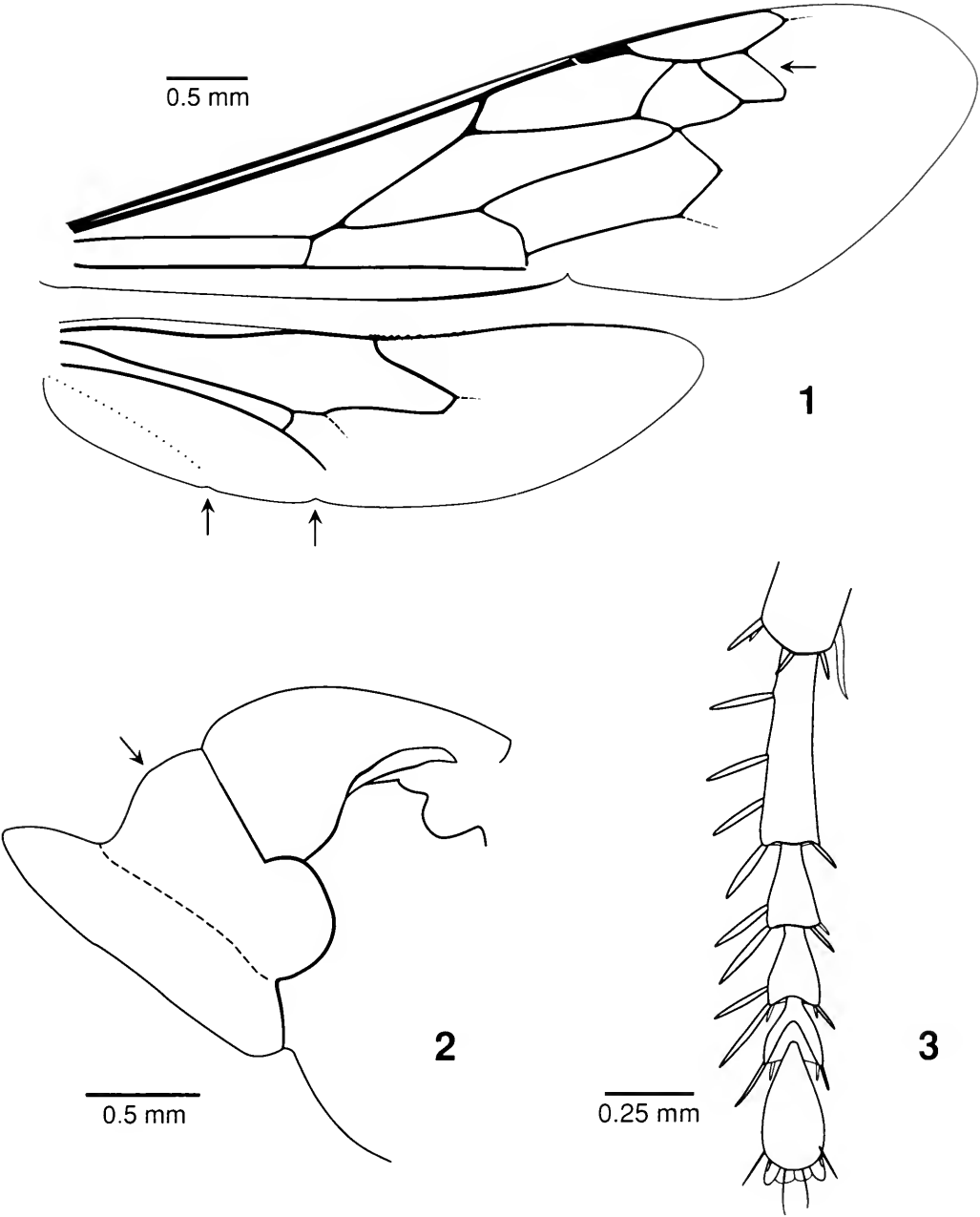
1. The frons has a median, slightly raised, flat area that is delimited by a lateral sulcus (Figs. 6, 10, 18, 22, 28, 31), the sulci being subparallel and close to the orbits. Similar sulci are found in some *Ancistromma* W. Fox, e.g., *capax* W. Fox, and in less specialized *Parapiagetia* Kohl such as *genicularis* (F. Morawitz) and *odontostoma* (Kohl), in which however, the frons is not raised.

2. The pronotal collar is rounded and reaches the scutum level, a condition also found in some *Gastrosericus*, e.g., *baobabicus* Pulawski and *eurypus* Pulawski. *Tachytella*, however, has three submarginal cells, whereas *Gastrosericus* has two.

3. The submarginal cell III in the forewing is essentially rhomboidal (Fig. 1), a previously unused character, with the anterior and posterior margins equal in length or nearly so; the proximal and distal margins are weakly sinuous, almost straight, nearly parallel to each other.

4. The hindwing jugal lobe is short and ends well before crossvein cu-a; consequently, the jugal and anal excisions are widely separated (Fig. 1). A similar condition is found in some specialized *Gastrosericus* such as *braunsi* Arnold, *herero* Pulawski, and *pulchellus* R. Turner (Pulawski 1995).

Description.—Bohart and Menke (1976) regarded *Tachytella* as monotypic and, consequently, considered as generic some structures that are found only in *aureopilosa* but not in the other two species (e.g., such male structures as the edentate inner mandibular margin, dentate clypeal free margin, and sterna VI–VIII with dense, erect setae). They thought that the pronotal collar not closely appressed to scutum



Figs. 1–3. Some of the generic characters of *Tachytella*. 1, fore and hindwing of *aureopilosa* (drawn from the holotype, the model Bohart and Menke 1976, used for their illustration); arrows indicate third submarginal cell, jugal excision, and anal excision. 2, anterior part of thorax of *aureopilosa* (arrow indicates pronotum). 3, foretarsus of female *nama*.

also was a generic character, but in fact it is only individual. The following redescription takes into account the three species now recognized and also some structures not considered previously. Included are those features that vary within other Larrini but are universal in *Tachytella*.

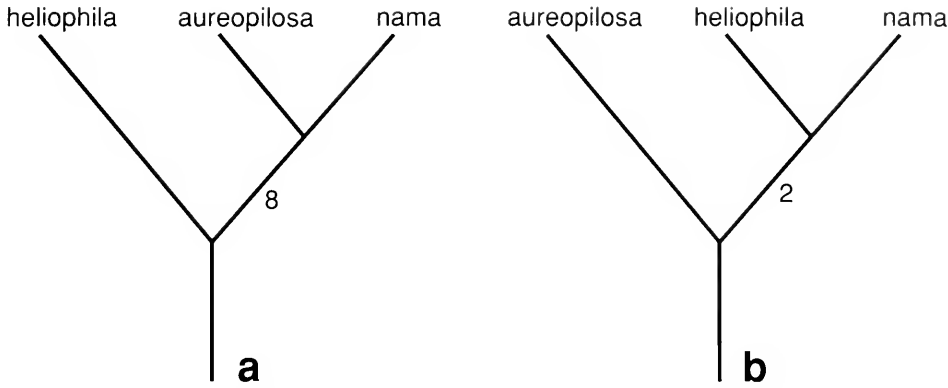
Labrum flat, not emarginate apically, not or barely protruding beyond clypeal free margin; prementum convex but not compressed laterally; stipes nearly flat. Mouthparts not elongate. Paramandibular process broadly separated from back side of clypeus (mandibular socket open). Posterior mandibular margin notched; notch delimited proximally by angulate apex of condylar ridge, and distally by marked, roundly expanded distal portion of adductor ridge. Clypeus produced into mesal lobe, free margin of lateral section concave. Antennal socket narrowly separated from frontoclypeal suture. Inner orbits convergent above. Frons flat, with no glabrous swelling above each antennal socket. Hindocellar scars elongate, broadly diverging anterolaterad (their long axes forming an angle of about 120–140°), shorter than distance that separates each one from midocellus. Occipital carina effaced just short of hypostomal carina. Pronotum anterodorsally with transverse groove; collar swollen, reaching level of scutum. Postspiracular carina evanescent, about as long as midocellar diameter. Episternal sulcus originating near middle of subalar fossa, ending well before reaching anteroventral mesopleural margin; scrobal sulcus absent; subalar fossa not margined below; metapleural flange not expanded. Axilla the usual shape, i.e., not expanded or carinate. Propodeum short, distance between spiracle and metanotum less than spiracle's length; dorsum setose throughout. No additional sclerites between metasternal apex and propodeum (no "propodeal sternum"). Forewing with three submarginal cells, none petiolate; recurrent veins separate or (some *aureopilosa*) forming short petiole. Hindwing crossvein

cu-a vertical (not inclined). Forecoxal apex not expanded into process. Hindcoxal dorsum: inner margin not carinate. Hindtibia not margined. Forebasitarsus and apical tarsomeres without ventral spines. Claws in each pair equal in size. Hindtarsomere II long ($0.6\text{--}0.7 \times$ hindtarsomere I). Base of tergum I variable: with or without short, oblique carina that extends from each anterolateral corner. Lateral carina of tergum I complete, reaching tergal hindmargin. Tergum II not carinate laterally. Body without erect setae (except setae on apical sterna in male of *aureopilosa*); those on propodeal dorsum inclined obliquely toward head.

Female. Inner mandibular margin with tooth. Forecoxa not carinate anteriorly, venter slightly convex; outer surface of foretibia without preapical spines. Foretarsus with rake that consists of stiff, flattened, widely spaced spines (four on forebasitarsus, two on foretarsomere II); tarsomeres IV: length more than apical width, apicoventral margin emarginate; tarsomeres V: apicoventral margin slightly arcuate. Claws without teeth. Tergum VI fairly convex: angle between lateral margin of tergum and lateral margin of pygidial plate, in side view about 30–40°. Pygidial plate well defined (margined laterally), rounded apically, sparsely punctate and with thin, inconspicuous setae (Figs. 9, 21, 30). Sting sheaths somewhat flattened dorsoventrally.

Male. Foretrochanter and forefemur not emarginate; forebasitarsus I with one rake spine (in basal half); outer, apical spine of foretarsomere II shorter than foretarsomere III; sterna without velvety patches; tergum VII carinate apicolaterally, not depressed apically; sterna III–VI impunctate at least mesally; sternum VIII rounded apically or (some *aureopilosa*) minimally emarginate. Venter of penis valve finely denticulate subapically (Figs. 17, 27, 35).

Character Polarization.—The tribe Larrini, of which *Tachytella* is a member, consists of two lineages, the subtribes Larri-



Figs. 4a and b. Cladograms showing hypothetical cladistic relationships of the three species of *Tachytella*; 2: modified cleft of inner mandibular margin, 8: penis valve with medioventral tooth.

na and Tachytina (Bohart and Menke 1976). The autapomorphy of Larrina is a unique frons: the midocellus is placed in a depression, and the transverse swelling delimiting the depression anteriorly joins a linear swelling along the inner orbit. The hindocelli are oriented along a transverse line, and the transparent lens remnant is horseshoe-like, with the two branches parallel and close to each other, apparently the plesiomorphic condition within the tribe. In Tachytina, the frons is the usual plesiomorphic condition, with no depression or swelling, but the hindocelli are oriented in a V-shaped pattern and the lens remnant is clearly derived: the anterior branch is longer than the posterior or (in *Parapiagetia*) the branches are roughly circular (open on the lateral side). Because of the shape of the lens remnant, *Tachytella* is a member of Tachytina, but its relationships within the subtribe are unclear. Bohart and Menke (1976) noted that *Tachytella* resembled *Ancistromma* and *Larropsis* Patton in the shape of the mandible, ocellar scar, female foretarsal rake, and male sternum VIII. None of these similarities, however, appears to be a synapomorphy. I have found no single derived character linking *Tachytella* with any of the other nine genera of the subtribe. For the purpose of this analysis, I regard the Larrina and the re-

maining Tachytina as the outgroup. The characters found in both *Tachytella* and the outgroup are considered plesiomorphic, unless there is strong evidence that they have been acquired independently. The characters present only in some *Tachytella* but not the outgroup are regarded as apomorphic. The character codings are: 0. ancestral, 1 and 2. derived. The following characters have been considered:

1. Female mandible inner margin: sub-basal tooth: 0. well defined, 1. inconspicuous, obtuse (as in *Tachytella aureopilosa*). The tooth is present in most members of the outgroup, but absent in *Larra* Fabricius, the subgenus *Motes* Kohl of *Liris* Fabricius, in *Parapiagetia*, several specialized *Gastrosericus*, and in two *Tachysphex* Kohl (*nefarius* Pulawski and *ramses* Pulawski). Because of their many specializations, none of these are likely to share a unique common ancestor with *Tachytella*, and consequently I regard the presence of a well defined mandibular tooth in *Tachytella* as ancestral.
2. Female mandible inner margin: cleft: 0. narrow, 1. shallow, obtusely angulate (as in *Tachytella aureopilosa*, 2. deep, broad (as in *Tachytella nama*). A cleft is present and narrow in most Larrinae (including *Tachytella heliophila*), but absent in *Larra*, the subgenus *Motes* of *Liris*, *Dalara* Ritse-



Fig. 5. Collecting localities of *Tachytella*.

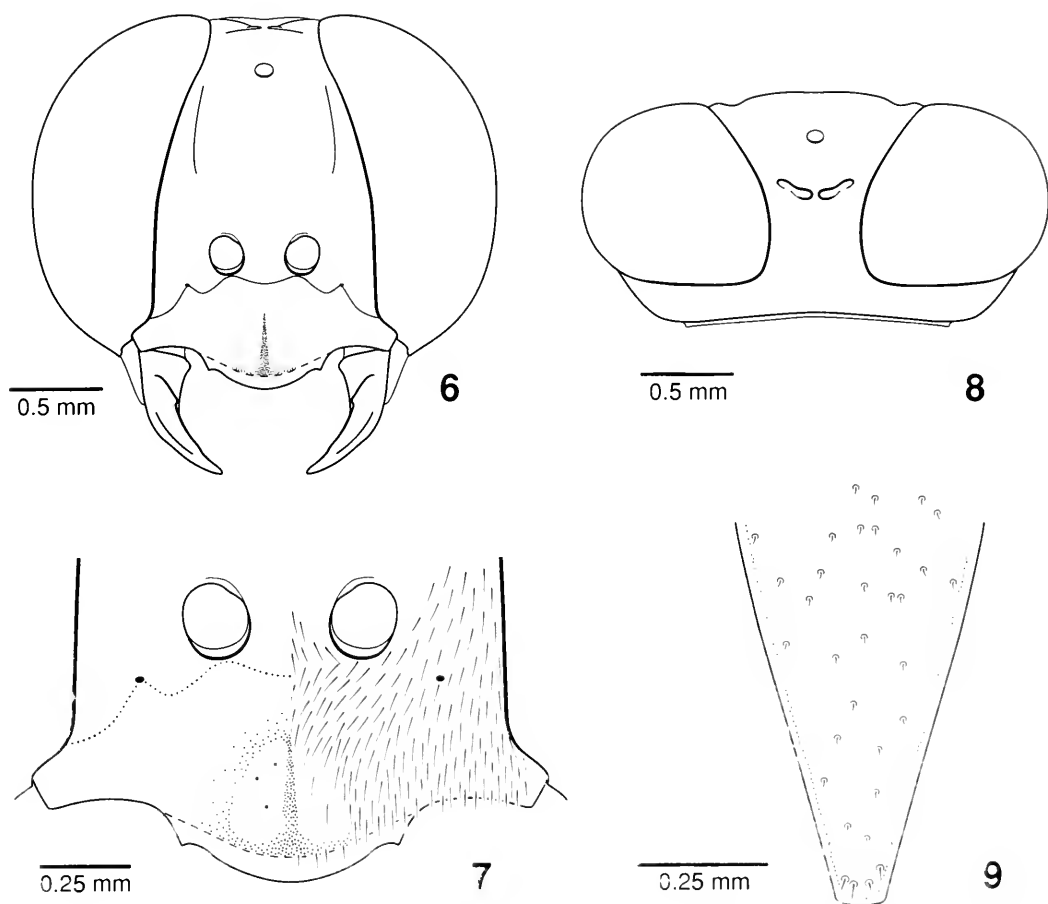
ma, *Paraliris* Kohl, *Holotachysphex*, many specialized *Gastrosericus*, *Parapiagetia genicularis* (F. Morawitz), *Tachysphex nefarius* and *ramses*. None of these is likely to share a unique common ancestor with *Tachytella*, and I therefore accept that a narrow cleft is ancestral in the latter genus. The broad, deep cleft is unique within the tribe.

3. Male clypeus: 0. without longitudinal swellings, 1. swellings present. The clypeal swellings of *aureopilosa* are unique within Larrinae and thus apomorphic.

4. Propodeum: 0. without V-shaped impression, 1. with V-shaped impression. The impression is unique to *Tachytella aureopilosa* and thus apomorphic.

5. Male foretarsus: 0. tarsomere II not expanded, 1. tarsomere II expanded. The expanded tarsomere of *Tachytella aureopilosa* is unique within the tribe and thus apomorphic.

6. Tergum I: 0. with a pair of short, basal carinae, 1. carinae absent. Within Larrini, the carinae are absent in *Gastrosericus*, *Holotachysphex*, *Kohliella*, *Parapiagetia*, *Tach-*



Figs. 6–9. *Tachytella aureopilosa*, female. 6, head frontally. 7, clypeus. 8, head dorsally. 9, pygidial plate.

ysphex, many *Tachytes* Panzer, and *Larrop-sis chilopsidis* (Cockerell and Fox). They are present in all other Larrini and other Sphecidae (those with a petiolate gaster are obvious exceptions). I therefore regard the absence of carinae in *Tachytella aureopilosa* as derived.

7. Male gaster: 0. sternal setae all short, 1. setae of sterna VI–VIII long, erect. Sternal setae are short, appressed in most Larrinae, but long, erect on apical sterna in many *Liris* and in *Tachytella aureopilosa*. These species are not likely to share a single common ancestor. In addition, the setal configuration of *T. aureopilosa* is unique and I regard it to be derived.

8. Penis valve: 0. without medioventral

tooth, 1. with medioventral tooth. This tooth, found in *Tachytella heliophila* and *nama*, is unique within Larrinae and thus apomorphic.

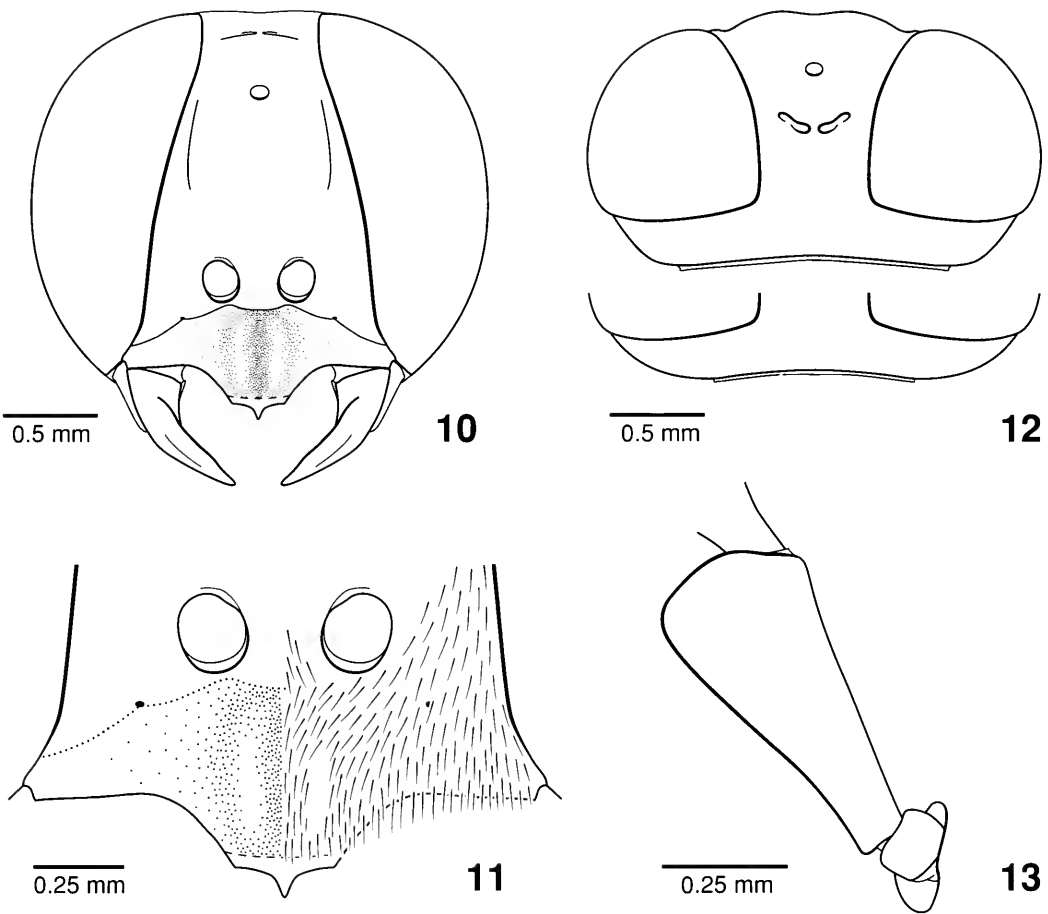
The following 5 characters cannot be polarized because both states are commonly found in the outgroup:

9. Gena: a. thin in dorsal view, b. thick in dorsal view.

10. Mesopleural vestiture: a. not concealing integument, b. concealing integument.

11. Hindtarsomere IV: a. length about 1.0 × apical width, b. length about 1.2–1.3 × apical width.

12. Pygidial plate of female: a. apex with a row of setigerous punctures,



Figs. 10–13. *Tachytella aureopilosa*, male. 10, head frontally. 11, clypeus. 12, head dorsally with outline of vertex showing variation. 13, scape.

b. apex without a row of setigerous punctures.

13. Male mandible: a. inner margin angulate, b. inner margin simple.

Cladistic Analysis.—Distribution of the 8 polarized characters is given below:

| | | | | | | | | |
|----------------------|---|---|---|---|---|---|---|---|
| Number: | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| ancestor: | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>aureopilosa</i> : | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| <i>heliophila</i> : | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>nama</i> : | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 |

Only two derived characters are found in more than one species: character 2 (a

modified cleft on inner mandibular margin) is shared by *aureopilosa* and *nama*, and character 8 (penis valve with medioventral tooth) by *heliophila* and *nama*. The cladogram resulting from character 2 (Fig. 4a) is *heliophila* + (*aureopilosa* + *nama*), the cladogram based on character 8 (Fig. 4b) is *aureopilosa* + (*heliophila* + *nama*). I see no reason to prefer one over the other.

Life History.—Unknown. The presence, in the female, of a foretarsal rake and a pygidial plate suggests ground nesting.

Geographic Distribution (Fig. 5).—Namibia and western half of South Africa.

KEY TO THE SPECIES

- 1. Propodeal dorsum with V-shaped impression that begins behind each spiracle and ends at hindmargin (impression inconspicuous in smallest individuals); tergum I basally without pair of short, oblique carinae. Female: clypeus (except basally) with finely, closely punctate median impression that separates two unsculptured, longitudinal areas (Fig. 6); inner mandibular margin with inconspicuous subbasal tooth (Fig. 6). Male: clypeus with pair of glabrous, longitudinal swellings, free margin with small, median tooth (Fig. 10); sterna VI-VIII with dense rows or tufts of erect setae (Fig. 15); penis valve without ventral tooth (Fig. 17) *aureopilosa* Brauns
- Propodeal dorsum without such impression; tergum I basally with pair of short, oblique carinae. Female: clypeal bevel without median row of small punctures; inner mandibular margin with well-defined subbasal tooth (Figs. 18, 28). Male: clypeus with no longitudinal swellings, free margin without small, median tooth; sterna without dense rows or tufts of erect setae; penis valve with ventral tooth (Figs. 27, 35) 2
- 2. Mesopleural vestiture conspicuous, fully concealing integument. Length of hindtarsomere IV $1.2-1.3 \times$ apical width. Female: free margin of clypeal lobe weakly arcuate, corner well defined but not prominent (Fig. 18); inner mandibular margin with usual, narrow cleft (Fig. 18). Male: clypeal lobe broad, nonprominent (Fig. 22); inner mandibular margin simple (Fig. 22) *heliophila* sp. n.
- Mesopleural vestiture inconspicuous, integument easily visible. Length of hindtarsomere IV about $1.0 \times$ apical width. Female: free margin of clypeal lobe sinuate, with prominent corner (Fig. 28); inner mandibular margin with broadly expanded cleft (Fig. 28). Male: clypeal lobe prominent, markedly narrowing anterad (Fig. 31); trimmal margin obtusely dentate (Fig. 31) *nana* sp. n.

DESCRIPTIONS OF SPECIES

Diagnostic characters for each species are given in the key and are not repeated individually in the descriptions below.

Tachytella aureopilosa Brauns
Figures 6-17

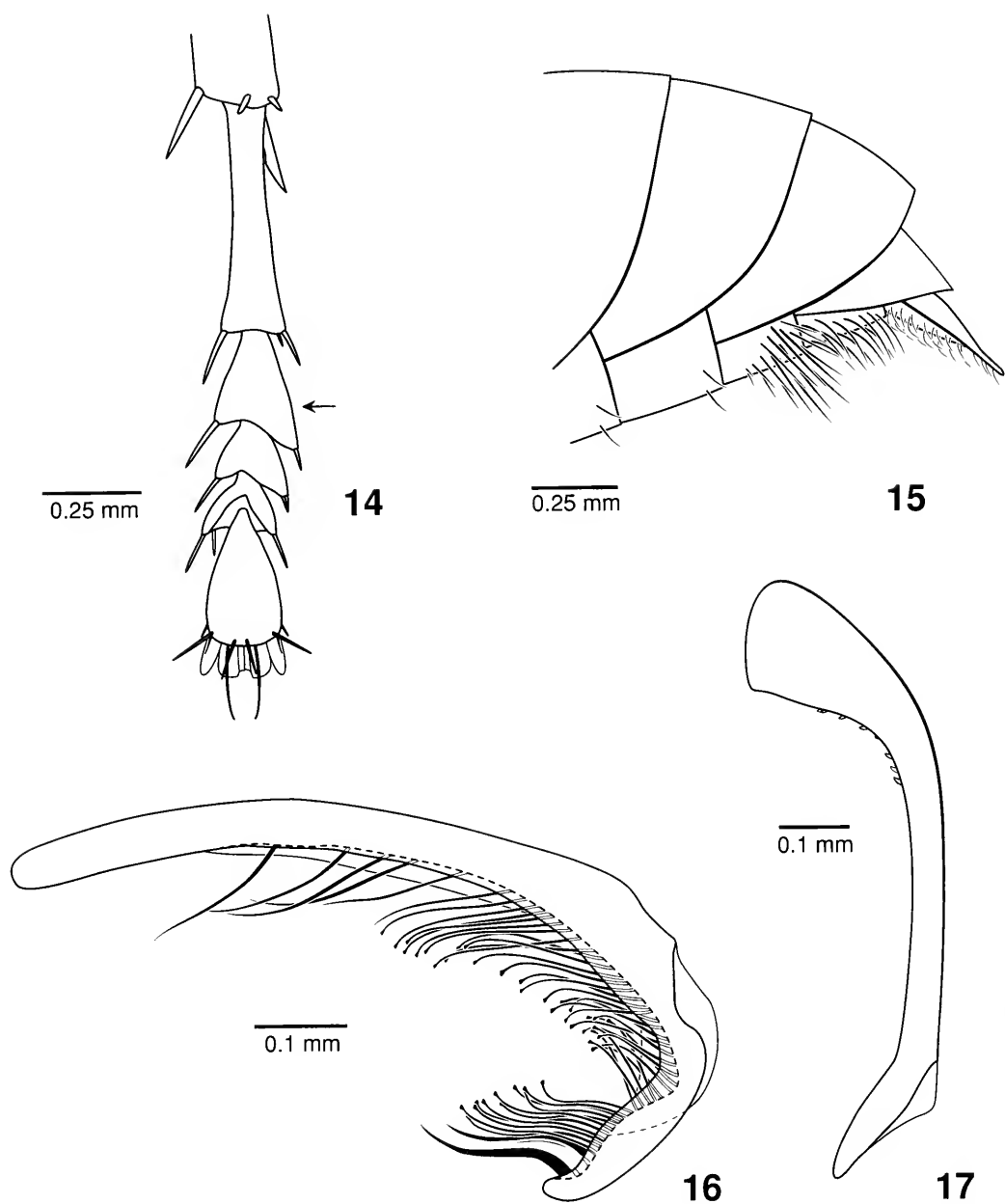
Tachytella aureo-pilosa Brauns, 1906:57, male, incorrect original hyphenation. Holotype: male, South Africa: Cape Province: Willowmore (TMP), examined.—Arnold 1923:218 (revision), 1930:5 (listed); Bohart and Menke 1976:231 (illustration of ocelli), 253 (illustration of male head), 255 (illustration of wings), 257 (listed), 258 (illustrations of pronotum and scutum), 268 (illustration of female foretarsus), 279 (illustration of male sternum VIII), 280 (illustration of male genitalia); Gess 1981:19 (South Africa: nesting probably in friable soils).

Tachytella aureo-pilosa race *nana* Arnold, 1936:29, female, male. Lectotype: male, South Africa: Cape Province: Resolution in Albany District

(TMP), present designation, examined. New synonym.—As *Tachytella aureopilosa nana*: Bohart and Menke 1976:253 (illustration of male head), 256 (new status, listed).

Synonymy.—Arnold (1936) described a var. *nana* for specimens that had red gastral segments I-III, shallower V-shaped impression on the propodeal dorsum, and truncate rather than shallowly emarginate male sternum VIII. Because these characters vary individually, I regard var. *nana* as a synonym of *aureopilosa*.

Description.—Gena thin in dorsal view (Figs. 8, 12). Vertex with triangular, glabrous, impunctate, dull area that extends from orbit toward midline. Head, thorax, coxae, and femora minutely punctate, punctures no more than 1 diameter apart, hence integument mat except for shiny clypeal swellings in male. Propodeal dorsum, in most specimens studied, with pair of impressions that meet postero-

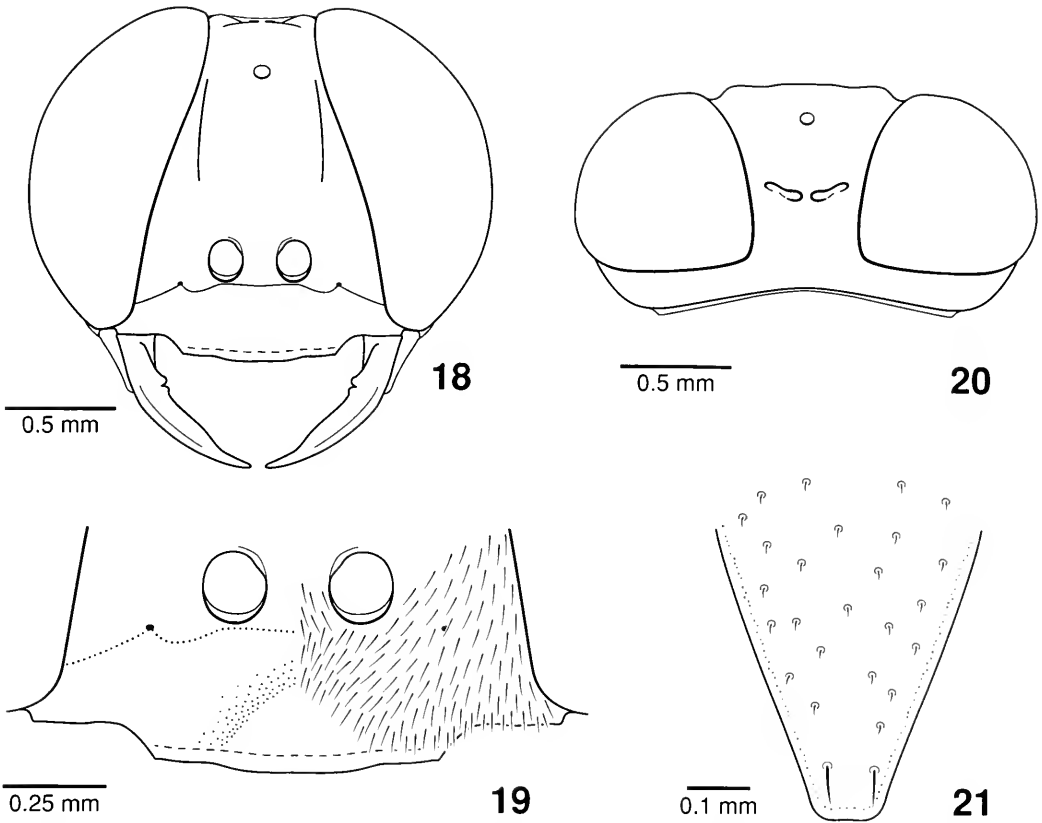


Figs. 14–17. *Tachytella aureopilosa*, male. 14, foretarsomere. 15, gastral apex in profile. 16, volsella. 17, penis valve.

mesally and delimit triangular area resembling propodeal enclosure of most Sphecidae (impressions barely visible in smallest specimens, apparently a result of allometric growth). Propodeal hindface not ridged. Femora and tibiae setose

throughout. Length of hindtarsomere IV about $1.0 \times$ apical width. Gastral segment I without basolateral, oblique carina.

Mesopleural vestiture concealing integument.



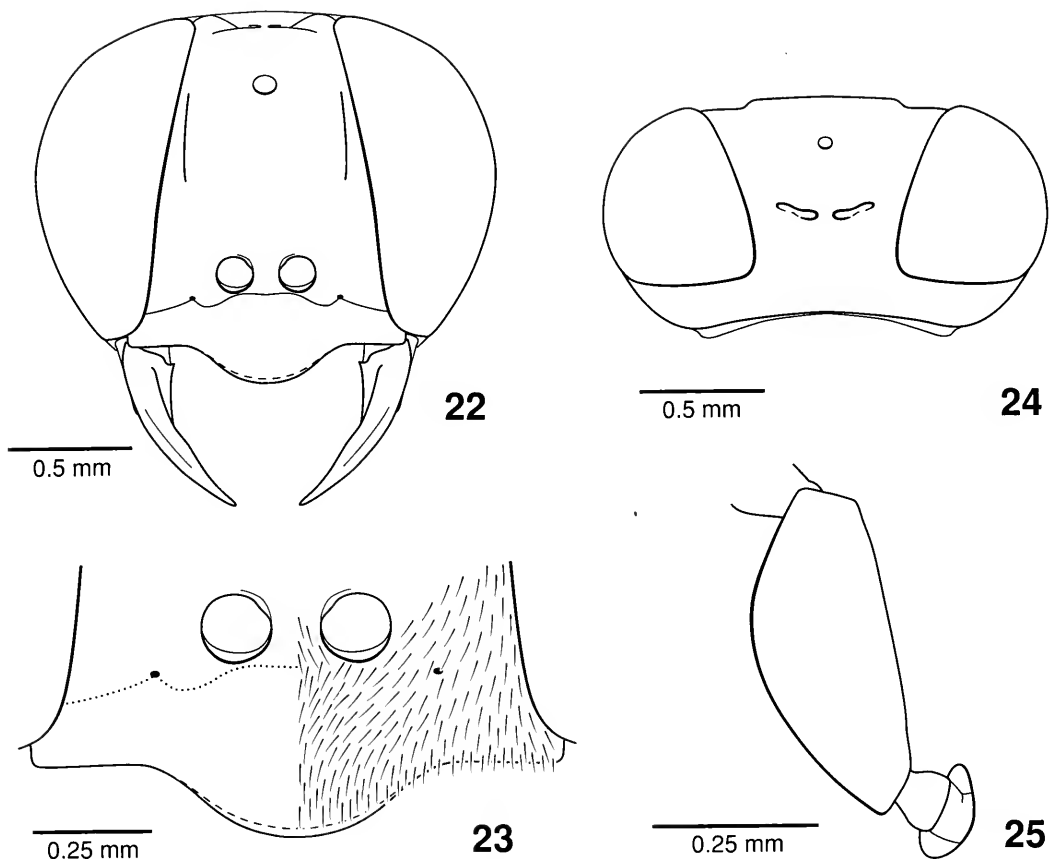
Figs. 18–21. *Tachytella heliophila*, female. 18, head frontally. 19, clypeus. 20, head dorsally. 21, pygidial plate.

Head and thorax black but the following are reddish: mandible (apical third dark), scape, tegula, and humeral plate. Gastral segment I to I–III red, remainder black. Mid- and hindfemora black, forefemur (except dorsally), tibiae and tarsi red. Wings nearly hyaline. Terga I–V silvery fasciate apically.

Female.—Mandible: inner margin divided by an obtuse angle into basal and distal portions, with shallow, obtusely angulate cleft. Clypeus with median, finely, densely punctate impression that separates two unsculptured, longitudinal areas (Figs. 6, 7); lobe free margin arcuate except markedly concave near corner, which is prominent (Figs. 6, 7). Length of flagellomere I $2.0 \times$ apical width. Vertex width $1.4 \times$ length. Tergum V punctate and se-

tose throughout. Pygidial plate with preapical row of setigerous punctures (Fig. 9). Length 7.3 mm

Male.—Mandible: inner margin simple, not angulate (Fig. 10). Clypeus (Figs. 10, 11): lobe free margin with median tooth, corner well defined but not prominent; distance between corners about $0.8 \times$ distance between corner and orbit; middle section with a pair of longitudinal swellings that are either microsculptured, dull, or unsculptured, shiny. Scape elongate, swollen apicoventrally (Fig. 13). Length of flagellomere I $1.7\text{--}1.8 \times$ apical width. Vertex width $1.6 \times$ length. Foretarso- mere II enlarged (Fig. 14). Tergum VII: punctures averaging about 1 diameter apart, some of them about 3 diameters apart. Apex of sternum VI, sternum VII, and VIII with



Figs. 22–25. *Tachytella heliophila*, male. 22, head frontally. 23, clypeus. 24, head dorsally. 25, scape.

erect setae; longest setae equal to basal mandibular width. Length: 6.1–8.5 mm. Volsella: Fig. 16. Penis valve without ventral tooth (Fig. 17).

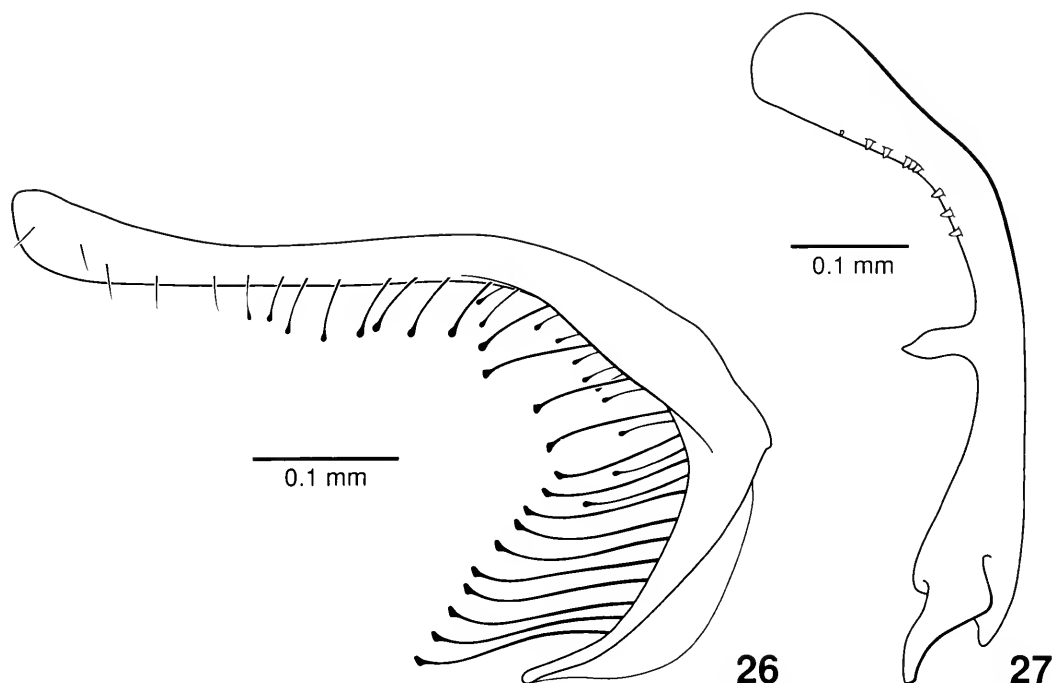
Geographic Distribution.—Western South Africa.

Records.—SOUTH AFRICA: **Cape Province:** Colesberg (1 female, SAM), Grahamstown: Hilton, sand pit (1 male, AMG), NE Ouberg Pass 31 road km NE Montagu at 33°39'S 20°18'E (1 male, AMG), Resolution in Albany District (1 female, 1 male, AMG; 1 male, SAM; 1 headless female, 1 male lectotype of *nana*, TMP), 10 km W Steinkopf (1 female, FSCA), Willowmore (1 male, TMP, holotype of *aureopilosa*), Worcester (3 males, BMNH; 1 male, USNM).

Tachytella heliophila Pulawski, new species
Figures 18–27

Name Derivation.—*Heliophila*, a Neolatin feminine adjective derived from two Greek words: helios, sun; and philos, a friend; with reference to the open, sunny habitat where the species was found.

Description.—Gena thin in dorsal view (Figs. 20, 24). Vertex without impunctate, triangular area. Head, thorax, coxae, femora and tibiae minutely punctate, punctures no more than 1 diameter apart, hence integument mat except for the unsculptured, shiny clypeal bevel. Propodeal hindface not ridged. Femora and tibiae setose throughout. Length of hindtarsomere IV 1.2–1.3 × apical width. Gastral segment I basolaterally with short, oblique carina.



Figs. 26 and 27. *Tachytella heliophila*. 26, volsella. 27, penis valve.

Mesopleural vestiture concealing integument.

Head and thorax black but the following are reddish: mandible (apical third black), clypeal bevel anteriorly, scapal venter apically, pronotal lobe, tegula, and humeral plate. Gaster red. Coxae and femora black (femora red apically), tibiae and tarsi red. Wings hyaline. Terga I–V silvery fasciate apically.

Female.—Mandible: inner margin with small subbasal tooth and narrow cleft (Fig. 18). Clypeus (Figs. 18, 19): free margin of lobe arcuate, corner angulate but not prominent; apicomedian portion of middle section shiny, practically unsculptured (with only a few microscopic punctures). Length of flagellomere I $2.75 \times$ apical width. Vertex width $1.7 \times$ length. Tergum V punctate and setose throughout. Pygidial plate with preapical row of setigerous punctures (Fig. 21). Foretibia without preapical spines. Length 6.6–7.5 mm.

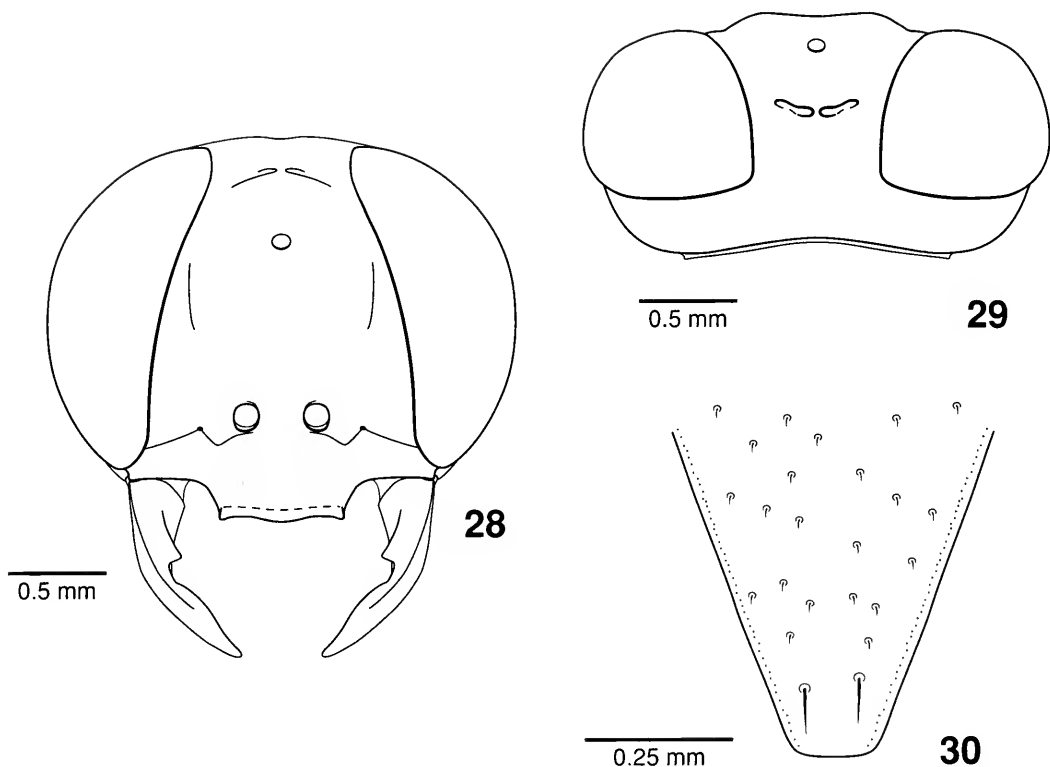
Male.—Mandible: inner margin simple,

not angulate (Fig. 22). Clypeus (Figs. 22, 23): lobe free margin arcuate, corner obtusely angulate; surface finely punctate and setose throughout except for narrow apical lip; distance between corners about $0.9 \times$ distance between corner and orbit. Scape swollen ventrally (Fig. 25). Length of flagellomere I $2.1 \times$ apical width. Vertex width $3.0 \times$ length. Tergum VII: punctures averaging less than one diameter apart. Length 6.4 mm. Volsella: Fig. 26. Penis valve with ventral tooth near mid-length (Fig. 27).

Geographic Distribution.—Known from a single area in Namib desert, western Namibia.

Records.—Holotype: female, Namibia: Karibib District: 65 km SW Usakos, 24 Feb. 1990, W.J. Pulawski (CAS).

Paratypes: NAMIBIA: **Karibib District**: 55 km SW Usakos, 1 Mar. 1990, W.J. Pulawski (1 female, CAS); 65 km SW Usakos, M. Schwarz, 24 Feb. 1990 (1 female, MS), 1 Mar. 1990 (1 female, MS; 1 male, CAS).



Figs. 28–30. *Tachytella nama*, female. 28, head frontally. 29, head dorsally. 30, pygidial plate.

Tachytella nama Pulawski, new species

Figures 28–35

Name Derivation.—*Nama*, a Hottentot tribe that immigrated from southern Africa into the central Namib; a noun in apposition to the generic name.

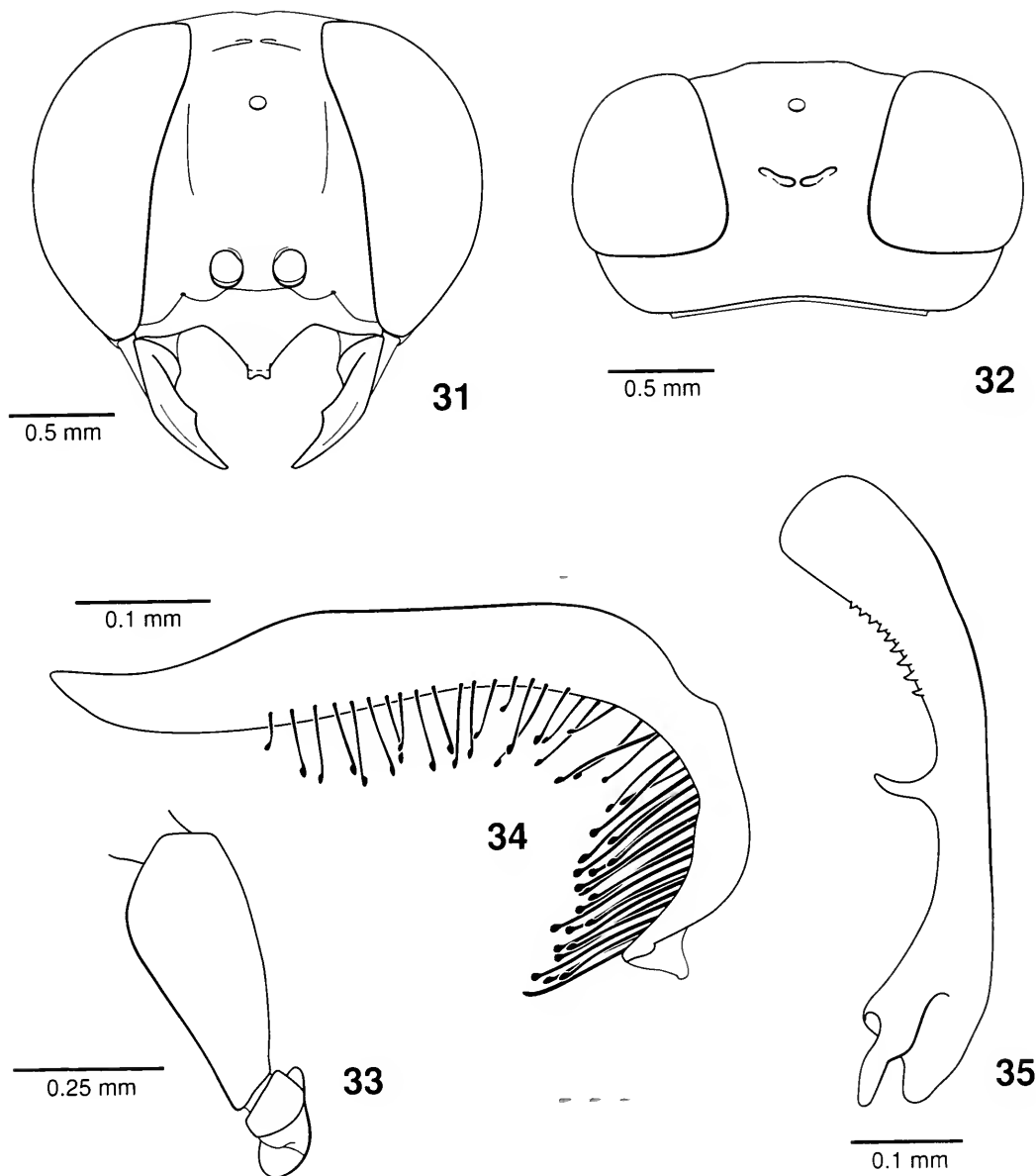
Description.—Gena thick in dorsal view (Figs. 29, 32). Vertex without impunctate, triangular area. Scutal punctures varying from mostly about 1 diameter apart (female from Goegap) to many diameters apart (most specimens). Mesothoracic venter with minute punctures that are several diameters apart. Propodeal hindface microscopically, densely ridged and with evanescent punctures. Fore- and midfemoral venter with a few, scattered punctures, asetose. Outer side of foretibia as well as mid- and hindtibial dorsum impunctate, asetose. Length of hindtarsomere IV about

1.0 \times apical width. Gastral segment I basolaterally with short, oblique carina.

Mesopleural vestiture inconspicuous, not concealing integument.

Head and thorax black except mandible yellowish basally and reddish distally, middle clypeal lobe of male reddish, male flagellum yellowish brown ventrally. Gastral segments I–III red, remainder black. Wings almost hyaline. Terga I–III silvery fasciate apically, but fasciae evanescent in most specimens.

Female.—Mandible: inner margin with subbasal tooth and broadly expanded cleft (Fig. 28). Clypeus (Fig. 28): lobe free margin sinuous, corner prominent; surface all or largely unsculptured (at most punctate basally). Length of flagellomere I 2.0 \times apical width. Vertex width 2.4 \times length. Tergum V with impunctate, gla-



Figs. 31–35. *Tachytella nama*, male. 31, head frontally. 32, head dorsally. 33, scape. 34, volsella. 35, penis valve.

brous apical depression. Pygidial plate with no preapical row of setigerous punctures (Fig. 30). Foretibia with two spines between inner surface and dorsum: one at midlength, the other at two thirds of length. Length 7.5 mm.

Male.—Mandible: inner margin obtusely angulate (Fig. 31). Clypeus (Fig. 31):

middle section markedly convex; lobe prominent, markedly narrowing anterad, with unsulptured apical part and shallowly emarginate anterior margin. Scape minimally swollen ventrally (Fig. 33). Length of flagellomere I $1.5 \times$ apical width. Vertex width $2.4 \times$ length. Tergum VII: punctures averaging more than one

diameter apart. Length 7.2 mm. Volsella: Fig. 34. Penis valve with ventral tooth (Fig. 35) near midlength.

Geographic Distribution.—Southern Namibia and northwestern South Africa.

Records.—Holotype: female, South Africa, Cape Province: Hester Malan [now Goegap] Nature Reserve near Springbok, 15–21 Oct. 1987, F.W. and S.K. Gess (AMG).

Paratypes: NAMIBIA: **Lüderitz District:** Namuskluft 88, 2716 Dd [= between 27°45' and 28°00'S and 16°45' and 17°00'E], collector unknown, 12–15 Sept. 1973 (1 female, SMW), 7–15 Oct. 1970 (1 male, SMW).

SOUTH AFRICA: Cape Province: Anenous, 29°14'30"S, 17°34'45"E, 11–13 Oct. 1988, D.W. Gess (2 females, AMG); Dikbome, Merweville Koup, [South African] Museum Expedition, Oct. 1952 (1 male, SAM); Hester Malan [now Goegap] Nature Reserve near Springbok, 15–21 Oct. 1987, F.W. and S.K. Gess (1 female, CAS); same data but 10–12 Oct. 1988 (1 male, AMG); between Kamieskroon and Springbok, [South African] Museum Staff, Oct. 1952 (2 females, CAS, SAM).

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Revision of the Ant Genus *Gnamptogenys* in the New World (Hymenoptera: Formicidae)

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Abstract.—Ants of the genus *Gnamptogenys* Roger in the New World are revised. The study is based mostly on worker morphology; 73 species are recognized, fifteen of which are new: *G. andina*, *G. boliviensis*, *G. brunnea*, *G. cuneiforma*, *G. ejuncida*, *G. extra*, *G. gentryi*, *G. laticephala*, *G. ilinani*, *G. nigrivitreata*, *G. pilosa*, *G. siapensis*, *G. stellae*, *G. transversa* and *G. volcano*. *G. ericae* is revalidated. In the present work sixteen names have been synonymized, and a morphological synopsis of the genus is given. The species range from southern U.S. to northern Argentina, but most are found in Central America and tropical South American forests. The evolutionary history of the genus is studied using phylogenetic systematics criteria. Six species groups are recognized: *striatula* group (22 species); *minuta* group (9 species); *rastrata* group (14 species); *sulcata* group (8 species); *mordax* group (17 species), and the *concinna* group (3 species). A key for the identification of workers is presented. Illustrations of morphological features supplement the key and descriptions.

INTRODUCTION

The genus *Gnamptogenys* Roger is a diverse group of ponerines with a distribution that covers the Neotropics, Indomalaysia and parts of the Nearctic and Australia. The genus as treated here is mostly the result of extensive synonymy by Brown (1958) in his revision of the Tribe Ectatommini. In this treatment, however, the *minuta* group species (= *Alfaria* Forel group of previous authors), are excluded and treated elsewhere (Brandão and Lattke 1990; Lattke 1992). Since Brown (1959), research on *Gnamptogenys* has consisted mostly of the description of new forms and scattered bits of ecological information. The only known fossils of the genus are two species reported from Dominican Amber by Baroni Urbani (1980). Lattke (1990) reviews the Venezuelan species and their natural history. Due to the growing number of specimens in collections, and the additional information published or accumulated in notes, a revision of the New World species seemed desirable.

MATERIALS AND METHODS

The revision is based primarily on worker morphology and the species have been defined conservatively because of considerable interpopulation variation. The criteria for judging allopatric populations as conspecific are as in Ward (1984: 131): if they are at least as dissimilar as closely related, sympatric species and are not connected by known intermediate forms. For a phylogenetic analysis, the genus *Ectatomma* Fr. Smith is used as an out-group in order to help determine the character state polarities. This genus is considered very close to *Gnamptogenys* and presents a greater number of primitive character states than either *Gnamptogenys* or *Rhytidoponera* Mayr (Lattke 1994). Species groups were determined and then compared using a character matrix (Table 1) and Farris's Hennig '86 v.1.5 phylogenetic inference program. The "ie-" option was used to generate the most parsimonious tree (Fig. 19) and a nelsen consensus

Table 1. Character state matrix

| | 123456789 | 0123456789 | 012345 |
|------------------------|-----------|------------|--------|
| <i>Ectatomma</i> | 000000000 | 0000000000 | 000000 |
| <i>G. haenschi</i> | 110001101 | 0010000000 | 012110 |
| <i>G. concinna</i> | 100011111 | 1110000001 | 000001 |
| <i>G. schmitti</i> | 100001021 | 1010000011 | 001010 |
| <i>strigata</i> sbgp. | 010010020 | 0000011201 | 000100 |
| <i>porcata</i> sbgp. | 000010020 | 0000011201 | 000100 |
| <i>striatula</i> sbgp. | 000010020 | 0000011200 | 000100 |
| <i>mordax</i> group | 111111121 | 111-011102 | 000011 |
| <i>sulcata</i> group | 110111121 | 1111011122 | 001011 |
| <i>rastrata</i> group | 110011120 | 0010111202 | 000010 |
| <i>minuta</i> group | 100011000 | 0010010001 | 110110 |

tree calculated from the 13 most parsimonious trees calculated by the "ie" option. Due to logistical difficulties, it was not possible to examine some types, this is especially true for European specimens. Thus this revision depends, in such cases, upon Brown's concept of the species involved, either through examining species determined by him during the course of his studies, reading the notes he took while visiting European collections in 1963 or from his 1958 revision. When type material was examined it is followed by a "T" in the species list.

Specimens were examined from or deposited in the following collections:

- BMNH The Natural History Museum, London, U.K.
- CMLB Colección Martha Lucia Baena, Cali, Colombia
- CASC California Academy of Sciences, San Francisco, California, U.S.A.
- CFFC Colección Fernando Fernández, Bogotá, Colombia
- CKWJ Colección Klaus Werner Jaffé, Universidad Simón Bolívar, Caracas, Venezuela
- CNIC Cornell University Insect Collection, Ithaca, New York, U.S.A.
- CUNB Colección Universidad Nacional, Bogotá, Colombia
- JTLC John T. Longino Collection, Evergreen College, Olympia, Washington, U.S.A.

- LACM Los Angeles County Museum of Natural History, Los Angeles, California, U.S.A.
- LEMQ Lyman Entomological Museum, McGill University, Ste. Anne de Bellevue, Québec, Canada.
- LNKD Landessammlungen für Naturkunde, Karlsruhe, Germany
- MCZC Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.
- MHNG Muséum d'Histoire naturelle, Geneva, Switzerland.
- MIZA Museo del Instituto de Zoología Agrícola, Universidad Central de Venezuela, Maracay, Venezuela
- MUSP Museu Universidade de São Paulo, São Paulo, Brazil
- NHMW Naturhistorisches Museum, Vienna, Austria.
- PSWC Philip S. Ward Collection, University of California, Davis, California, U.S.A.
- USNM United States National Museum, Washington, D.C., U.S.A.
- WPMC William P. MacKay Collection, University of Texas, El Paso, Texas, U.S.A.

Measurements and Indices

Morphological measurements were made at magnifications of up to 100× with an ocular micrometer on a Wild M5 stereoscope. Since ratios derived from the measurements are conveniently scaled indices by themselves, the orthodox procedure of multiplying them by 100 was not followed. The measurements follow those of Latke (1990).

- HL Head length: midline length of head proper, measured in full-face (dorsal) view, from the anterior clypeal margin to the midpoint of a line drawn across the vertexal margin.
- ML Mandibular length: length of

closed mandibles, from the anterior clypeal margin to the apices of the mandibles, measured in the same plane as HL.

- SL Scape length: length of the first antennal segment, excluding the neck and basal condyle.
- ED Eye Diameter: diameter of eye, measured along its long axis in lateral view
- HW Head width: maximum width of head, measured in full-face (dorsal=frontal) view, excluding the eyes.
- WL Weber's length of the mesosoma (alitrunk): diagonal length measured in lateral view, from the anterior margin of the pronotum (excluding collar) to the posterior extremity of the metapleural lobe.
- CI Cephalic index: HW/HL
- MI Mandibular index: ML/HW
- SI Scape index: SL/HW
- OI Ocular index: ED/HW
- SSC Scape setal count: the number of standing hairs (not pubescence), i.e. those forming an angle of 45° or more with the cuticular surface, visible in outline on the upper surface of the scape, with the line of view at right angles to the plane of funicular inflexion.

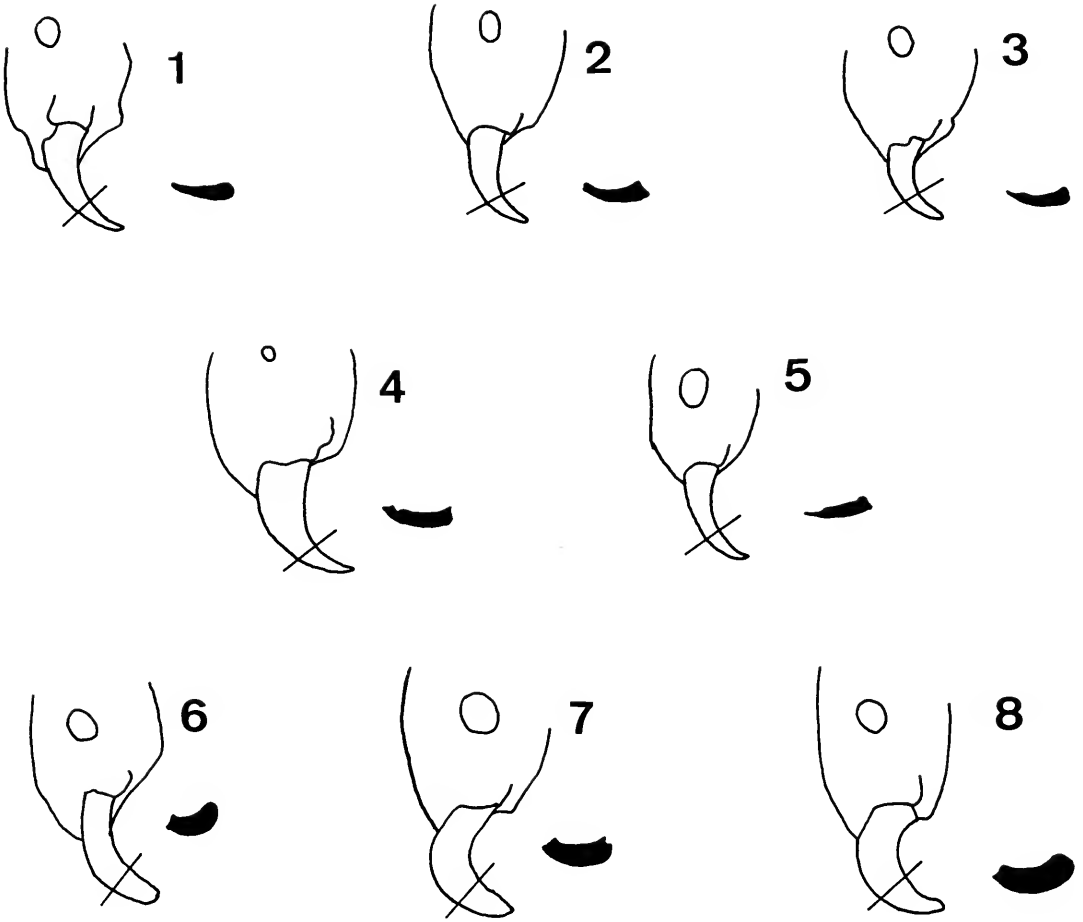
New World *Gnamptogenys* Roger

Generic Synopsis (Worker).—Sculpture consisting mostly of even parallel costae, costulae or strigae, occasionally rugose; distinct dorsomedian cephalic carinae usually absent, at most never extending more than half-way between clypeus and vertex; eyes at midlength of head or posterad, surrounded by a fine groove; lobes of frontal carinae broadly convex and partially raised, incompletely covering antennal condyles (except *minuta* group); funiculus filiform or incrassate, never with a distinct club; anterior clypeal border with narrow lamella of variable length; mesepisternum anteroventrally bordered by

narrow lamella; pronotum unarmed, without protuberances; propodeal spiracles round or slightly ovoid, never slit-like; transverse sutures and grooves on mesosomal dorsum present or absent; mesonotum never prominently convex and bulging; anterior prosternal process bidentate; anterior mesepisternal process produced as thin triangular lobe with pointed or bluntly pointed apex; metepisternum with deep posterior cleft for petiolar insertion and continuous with open metacoxal fossae; metepisternal process located anterad of cleft and of variable development; metacoxal dorsum usually with denticle, lobe or tubercle, absent in some species; helcium protruding medianly on anterior postpetiolar face; tergite of helcium much larger than sternite; fortibial apex lacking stout moveable setae; outer border of foretarsal comb (opposite calcar) usually with single prominent seta; meso- and metatibial spurs one or two (weakly developed), barbate or simple; empoida lacking. In most species the pretarsal claws are bidentate on all legs, and the median tooth may vary in its position among species, and the claws may not necessarily be alike on all legs. In small species the claws may be hard to observe.

Malpighian tubule number six (Brown 1988). The genus is so diverse that characterizing it can be difficult. The following characters can be considered synapomorphies of the genus which distinguish it from its closest relatives: *Ectatomma* and *Rhytidoponera*: the single stout moveable seta on the foretibial apex and a spine or tubercle on the metacoxal dorsal surface. This former trait is lacking in some species. The following combination of characters are synapomorphic for the genus if one excludes the problem species discussed further on in the text: inconspicuous metanotum, disappearance of the median cephalic carina, lack of row of stout setae on foretarsal base opposite the strigil, leaving only one seta.

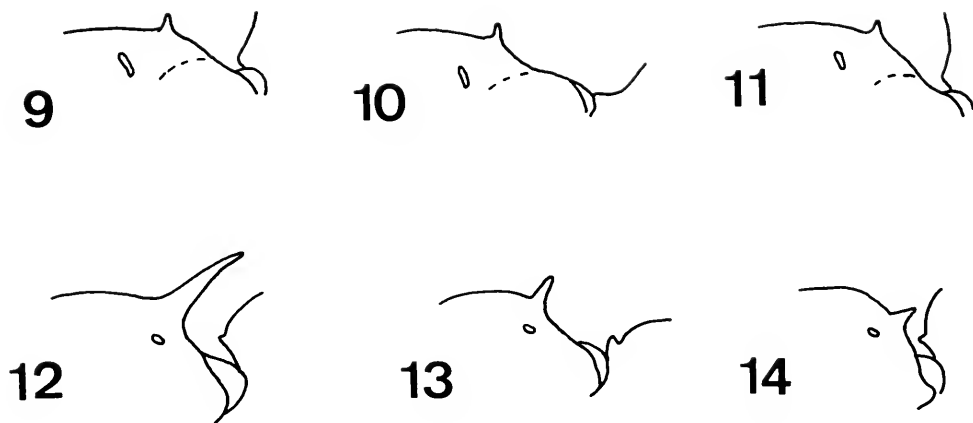
Characters.—The choice of characters for



Figs. 1-8. Lateral view of mandibles and anterior section of head of *Ectatomma* and *Gnampptogenys*. Transverse section of mandible depicted in black with chewing border to the left and frontal surface below. 1, *E. ruidum*; 2, *G. porcata*; 3, *G. moellerius*; 4, *G. haenschii*; 5, *G. triangularis*; 6, *G. mordax*; 7, *G. tortuolosa*; 8, *G. concinna*.

use is complicated by convergence in several instances. Some character states considered apomorphic have apparently been reached independently by one or two species in different lineages. Examples are the smooth and shining scapes of *G. rastrata* and of *G. mordax*, or the conspicuous metanotal groove of *G. bisulca* and *G. brunnea*. There are also some apparent reversals, as well as retention of plesiomorphies present in the outgroup. But these cases are few, isolated and do not represent the major trends of their respective species groups. Therefore, they were not taken into account for defining group character

states. Mandibular shape is an apparent useful indicator of phylogenetic trends, with the general direction being from plesiomorphic triangular mandibles to apomorphic forms as subtriangular or subfalcate. Subtriangular mandibles have been independently derived in the *haenschii*, *sulcata*, and *mordax* groups, as indicated by other mandibular traits such as the configuration of the chewing border, sculpture and cross section. In the last two groups (Figs. 6-8), the mandibular cross section reveals thick, robust mandibles as opposed to the slim cuneiform section of *G. haenschii*, which is the plesiomorphic state

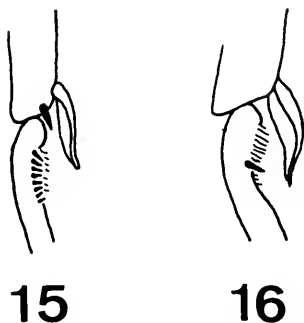


Figs. 9–14. Lateral view of propodeum of *Ectatomma* and *Gnampptogenys*. 9, *E. lugens*; 10, *E. quadridens*; 11, *E. tuberculatum*; 12, *G. bispinosa*; 13, *G. perspicax*; 14, *G. triangularis*.

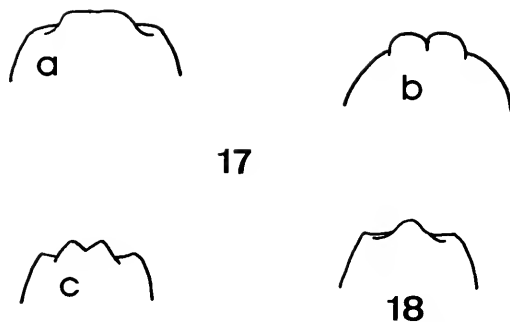
exhibited by the outgroup and the *striatula* and *rastrata* groups (Figs. 1–5). The subpetiolar process in its primitive state is triangular, lobe-like and anteriorly protruding. Modification has been towards a subquadrate shape, but some species, such as *G. striatula*, exhibit both conditions, and in the derived *mordax* subgroup the triangular subpetiolar process is probably a reversal.

Some characters are shared by the outgroup and certain groups or subgroups of *Gnampptogenys*. Two of these are particularly important: the propodeal denticles and the setae on the foretarsal base. The

propodeal denticles of *Ectatomma* may be absent in some species and when present, they are quite modest, usually lobe-like and directed dorsally. The declivitous propodeal face runs evenly and directly to the denticular apex (Figs. 9–11). The denticles in the *rastrata* group are stout and inclined posterad, and their base forms a more abrupt separation from the propodeal declivity (Figs. 12–14). With the exception of a few highly derived species, propodeal denticles are lacking in *Rhytidoponera* and the *striatula* group of *Gnampptogenys*. This suggests that the presence of propodeal denticles is probably independently derived in *Ectatomma* and *Gnampptogenys* and consequently was lacking in the ancestral stock of this group of genera. For this reason this state has been given value 0 in the character matrix for *Ectatomma*. The base of the foretarsus, in the concavity opposing the strigil, has an outer row of stout setae in *Ectatomma*, but only one prominent seta in most *Gnampptogenys* (Figs. 15–16). The exceptions are all the minuta-group species besides three other species, and each of these exceptions are unique within the genus as will be discussed later on. The brief anterior peduncle of the petiole, typical of *Ectatomma* is considered plesiomorphic for the *porcata* subgroup,



Figs. 15–16. Outer lateral view of apex of tibia and base of tarsus of foreleg. 15, typical configuration in *Ectatomma* with single calcaria on tarsal apex and row of setae in foretarsal concavity; 16, same in most *Gnampptogenys* with only one stout seta on foretarsal concavity.



Figs. 17–18. Ventral view of the anterior postpetiolar process. 17: a, *G. triangularis*; b, *G. haenschii*; c, *G. striatula*. 18, *G. sulcata*.

but autapomorphic for the *mordax* subgroup. The following characters were taken into account for all the species groups or individual species in the matrix, but have been restricted to the *minuta* subgroup of the *minuta* group (Lattke 1991). Characters 8, 17, 18 were considered non-additive.

The following character states were taken into account:

1. Head shape in frontal view: 0=wider posterad than anterad, 1=subquadrate/other.

2. Funiculus shape: 0=filiform to subfiliform, 1=incrassate.

3. Scape length: 0=surpassing vertexal border (Figs. 39, 41), 1=does not surpass, at most reaching the vertexal border (Fig. 43).

4. Scape sculpture: 0=scapes with appreciable sculpture, 1=smooth and shining. The aforementioned sculpture usually consists of punctulae, punctae or striae.

5. Development of the clypeal lamella: 0=poorly developed, very short, 1=well developed. This character refers to how far anterad the lamella extends. In poorly developed cases the longitudinal cephalic costulation is not clearly delimited from the lamella.

6. Shape of anterior clypeal margin: 0=convex clypeus (Figs. 33, 37, 39, 41), 1=straight/concave (Figs. 34–36, 62, 64).

7. Shape of lateral extremities of anterior clypeal lamella: 0=softly curves (Figs.

33, 37, 39, 41), 1=angular/pointed (Figs. 34–35).

8. Presence of median clypeal carinae: 0=present, 1=variable, 2=absent or indistinct.

9. Mandibular shape: 0=triangular (Figs. 39, 41), 1=subtriangular/subfalcate (Figs. 43, 54, 69, 62).

10. Shape of cross section at apical one third of mandible: 0=thin and cuneiform (Figs. 2–5), 1=wide and robust (Figs. 6, 7).

11. Sculpture of mandibular dorsum: 0=striae/rugulae (Fig. 54), 1=smooth and shining (Fig. 43).

12. Development of promesonotal suture: 0=deeply impressed, cleaving sculpture (Figs. 46, 49, 52), 1=weakly impressed, effaced (Fig. 55).

13. Development of metanotal groove: 0=deeply impressed (Fig. 55), 1=weak to effaced (Figs. 46, 49, 52).

14. Development of propodeal denticles: 0=absent (Figs. 46, 49, 52), 1=present (Figs. 12–14).

15. Position of spiracle on propodeal side, in lateral view: 0=anterad, well separated from declivitous propodeal face, 1=posterad, close to declivitous propodeal face.

16. Presence of setae on foretarsal base opposite the strigil: 0=row of stout setae (Fig. 15), 1=one prominent seta only (Fig. 16).

17. Development of dorsal metacoxal

process: 0=absent, 1=variable, 2=well developed (Figs. 46, 49).

18. Shape of the metasternal process: 0=stout denticles or tubercles, 1=acicular, straight denticles, 2=acicular, arched denticles.

19. Shape of petiolar node: 0=erect and high node (Figs. 46, 49, 52), 1=high and posterad, 2=subcylindrical/other (Figs. 61, 63, 65).

20. Petiolar spiracles: 0=directed obliquely; 1=directed ventrally.

21. Petiolar spiracles: 0=-at the same level as the surrounding integument; 1=in a distinct depression.

22. Shape of postpetiolar process in lateral view: 0=broad (Fig. 17), 1=bluntly pointed (Fig. 18).

23. A brief median carina on the dorsum of the postpetiolar process: 0=absent, 1=present. This is a low carinae that starts at the anterior margin of the process and briefly extends posterad.

24. Abdominal segment IV: 0=with a ventral stridulitrum, 1=without a ventral stridulitrum. Usually recognizable as a longitudinal band that refracts light into rainbow colors.

25. Shape of the fourth abdominal segment: 0=ventrally reflexed (Fig. 55), 1=straight (Fig. 44).

Species Groups.—Within the New World *Gnamptogenys* six species groups are defined here: *striatula*, *sulcata*, *concinna*, *minuta*, *mordax* and *rastrata*. The internal classification of the genus is depicted in Table 2. The characters used in defining the following informal groupings are diverse, thus they may or may not be synapomorphies. A question mark following the species name means that its position within the group is not clear.

1. *striatula* group: mandibles triangular with rugulae or striae on frontal surface; convex anterior clypeal margin; scapes usually surpassing vertexal margin, sculpturing punctate or vermiculate, never smooth and shining; eyes slightly behind cephalic midlength; head wider posterad

Table 2. Internal classification of *Gnamptogenys* (except *minuta* group)

| | |
|---|--|
| <i>striatula</i> group | |
| <i>porcata</i> subgroup: | <i>acuta</i> , <i>brunnea</i> , <i>ejuncida</i> , <i>extra</i> , <i>gentryi</i> , <i>gracilis</i> , <i>nigrivitre</i> a, <i>pilosa</i> , <i>pleurodon</i> , <i>porcata</i> |
| <i>striatula</i> subgroup: | <i>ammophila</i> , <i>moelleri</i> , <i>striatula</i> |
| <i>strigata</i> subgroup | |
| <i>strigata</i> complex: | <i>andina</i> , <i>bisulca</i> , <i>ilimani</i> , <i>pittieri</i> , <i>strigata</i> |
| <i>haytiana</i> complex: | <i>haytiana</i> , <i>mina</i> , <i>reichenspergi</i> , <i>relicta</i> |
| <i>rastrata</i> group | |
| <i>rastrata</i> subgroup: | |
| <i>bispinosa</i> complex: | <i>bispinosa</i> , <i>perspicax</i> |
| <i>rastrata</i> complex: | <i>cuneiforma</i> , <i>ingeborgae</i> , <i>lanei</i> , <i>lineolata</i> , <i>lucaris</i> , <i>mecotyle</i> , <i>menozzi</i> , <i>rastrata</i> , <i>triangularis</i> |
| <i>banksi</i> subgroup: | |
| <i>banksi</i> complex: | <i>laticephala</i> , <i>mediatrix</i> |
| <i>semiferox</i> complex: | <i>semiferox</i> |
| <i>sulcata</i> group | |
| <i>sulcata</i> subgroup: | |
| <i>fernandezi</i> complex: | <i>fernandezi</i> |
| <i>sulcata</i> complex: | <i>acuminata</i> , <i>curvoclypeata</i> , <i>tortuolosa</i> |
| <i>ericae</i> subgroup: | |
| <i>ericae</i> complex: | <i>ericae</i> |
| <i>lucaris</i> complex: | <i>lucaris siapensis</i> |
| <i>volcano</i> complex: | <i>volcano</i> |
| <i>mordax</i> group | |
| <i>regularis</i> subgroup: | |
| <i>hartmani</i> complex: | <i>bruchii</i> , <i>hartmani</i> , <i>transversa</i> |
| <i>regularis</i> complex: | <i>hornii</i> , <i>nana</i> , <i>pristina</i> , <i>regularis</i> , <i>rimulosa</i> |
| <i>annulata</i> complex: | <i>annulata</i> , <i>kempfi</i> |
| <i>mordax</i> subgroup: | <i>continua</i> , <i>boliviensis</i> , <i>interrupta</i> , <i>mordax</i> , <i>stellae</i> |
| <i>alfaroi</i> subgroup: | <i>alfaroi</i> |
| <i>levinates</i> subgroup: | <i>levinates</i> |
| <i>concinna</i> group | |
| <i>concinna</i> , <i>haenschi</i> , <i>schmitti</i> | |

than anterad; propodeal spiracle close to declivity; anterolateral propodeal declivity without spines or tubercles; anterior prosternal process broadly concave medianly; metacoxal dorsum always with denticle or lobe; high petiolar node; relatively wide anteroventral postpetiolar process; second

gastric segment ventrally arched. Most seem to be generalist predators, but nothing is yet known about the diet of the *striatula* subgroup species.

Three subgroups are recognizable: 1) *striatula* subgroup: petiolar node erect and sessile; subpetiolar process variably shaped, either subquadrate or triangular and projecting anterad in lateral view. 2) *porcata* subgroup: petiolar node posteriorly inclined, with short anterior peduncle; subpetiolar process lobe-like, projecting anterad in lateral view. 3) *strigata* subgroup: petiolar node variably shaped; subpetiolar process subquadrate with a cuneiform ventral edge (Fig. 30) as opposed to the uniformly parallel sides of the other *striatula* group species (Fig. 29). Many of the species have their propodeal spiracles elevated on small prominences. Most species are smaller in size than those of other subgroups and all are cryptobiotic leaf-litter inhabitants. Two species complexes can be pointed out in this subgroup: a) *strigata* complex: cephalic vertex sculptured; no distinct propodeal lobes; petiolar node not parallel-sided in lateral view, anterior margin usually convex (Figs. 40, 57). All species inhabit cloud forests, mostly of the Andes, with the exception of one found in the Cordillera de la Costa of Venezuela. b) *haytiana* complex: cephalic vertex mostly smooth and shining; small propodeal lobes present; petiolar node strongly compressed with subparallel anterior and posterior faces (Fig. 21); some species have modified sculpturing from the usual costulate patterns of the genus. Most species inhabit the Amazon-Orinoco river basin, except for one species found on Hispaniola Island. Kugler (1991) obtained similar results studying the sting apparatus of *brunnea*, nr. *strigata*, *porcata*, *moelleri* and *gracilis*. They were the only members of the *striatula* group included, as defined above, and were grouped together.

II. *rastrata* group: head subquadrate or wider anterad than posterad in frontal

view; anterior clypeal margin usually straight; mandibular front usually striate or rugulose, sometimes smooth; scapes usually surpassing vertex, sometimes with longitudinal rugulae, vermiculate or smooth and shining; promesonotal suture feebly impressed to absent, never totally dividing sculpture; metanotal suture well impressed; propodeum usually armed with denticles or spines; petiolar node low; subpetiolar process shape variable, usually projecting anterad but sometimes subquadrate; metacoxal teeth always present, usually acicular; second gastric segment ventrally arched. The ants of this group are specialized millipede predators and can be subdivided into two subgroups. 1) *rastrata* subgroup: mandibles triangular. Within the subgroup two complexes are defined: a) *bispinosa* complex: large species, anterior clypeal margin convex, propodeal teeth above level of spiracles; anterior lobe of subpetiolar process prominent. b) *rastrata* complex: smaller species; anterior clypeal margin straight; propodeal teeth at same level as spiracles; subpetiolar process subquadrate. 2) *banksi* subgroup: mandibles subfalcate to falcate. Two species complexes are defined. a) *banksi* complex: metacoxae and propodeum with denticles. b) *semiferrox* complex: metacoxae and propodeum lacking denticles. In a study of the sting apparatus of several species of *Gnamptogenys* Kugler (1991) grouped *triangularis* and *bispinosa*, the only members of the *rastrata* group as defined above, into one group.

III. *mordax* group: antennal scapes usually do not reach vertex and are compressed, smooth and shining; mandibles subtriangular to subfalcate with front smooth and shining; head subquadrate to elongate; mesosoma mostly parallel sided; small propodeal lobes frequently present, denticles absent (except one species); metacoxal denticles or lobes frequently lacking; second gastric segment straight, without ventral arching. Considerable inter-population variability in the average size

is observed in species of this group. The group can be divided into 4 subgroups: 1) *regularis* subgroup: mandibles subtriangular; anterior clypeal border straight and usually with laterally acutely pointed lamella; no transverse dorsal mesosomal sutures; petiolar node lacking anterior peduncle; subpetiolar process subquadrate. Within this subgroup three species complexes are recognizable. a) *hartmani* complex: mandibles triangular to subtriangular, frontal surface partially sculptured; vertical sculpturing on declivitous propodeal face; b) *regularis* complex: mandibles subtriangular, their frontal sides smooth and shining; vertical sculpturing on declivitous propodeal face; c) *annulata* complex: mandibles subtriangular, front smooth and shining; horizontal sculpturing on propodeal declivity. 2) *mordax* subgroup: mandibles subfalcate, frontal surface smooth and shining; anterior clypeal margin concave with rounded lamellar sides; well impressed metanotal groove; petiolar node slightly pedunculate; subpetiolar process projects anterad. 3) *alfaroi* subgroup: mandibles triangular, head prominently elongate; denticles on propodeum. The elongate head and armed propodeum makes this subgroup quite distinct from the others. 4) *levinates* subgroup: subtriangular mandibles, frontal surface sculptured; scapes surpassing vertex; subpetiolar process subquadrate. Its clypeus projects anterad more than in any extant species of the group.

IV. *sulcata* group: mandibles subtriangular, front smooth and shining; head subquadrate; anterior clypeal border usually straight; lamella usually laterally angular; scapes smooth and shining; metacoxal denticles wanting in some species; usually no transverse mesosomal sutures; petiolar node low, lacking peduncle; metasternal process acicular and arched; second gastric segment relatively straight; anteroventral postpetiolar process relatively narrow and bluntly pointed, in contrast with wider process of other species. Two sub-

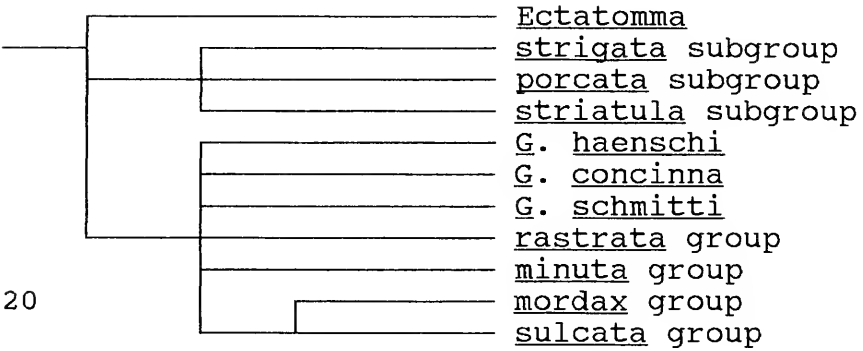
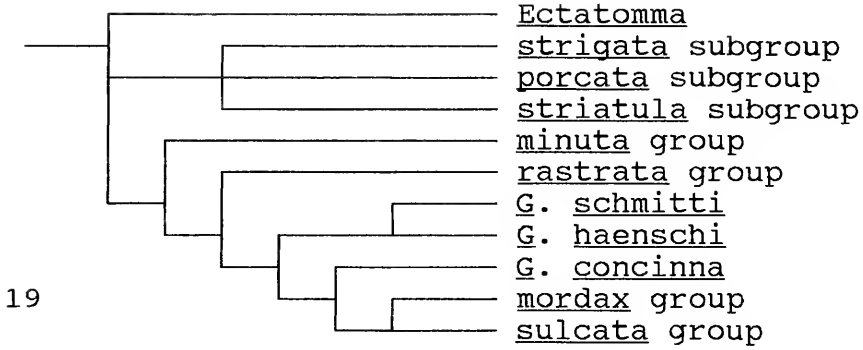
groups can be pointed out. 1) *sulcata* subgroup: posterior face of petiolar node with horizontal costulae. Two species complexes are recognizable: a) *fernandezi* complex: mandibles triangular; clypeal lamella convex. b) *tornata* complex: mandibles subtriangular; clypeal lamella straight. 2) *sulcata* subgroup: posterior node face with longitudinal costulae. This subgroup is made up of three complexes. a) *ericae* complex: clypeal lamella laterally acutely angulate; mandibles subtriangular. b) *lucaris* complex: clypeal lamella laterally rounded; mandibles subtriangular. c) *volcano* complex: clypeal lamella laterally obtusely angulate; mandibles triangular.

V. *concinna* group: head subquadrate; scapes surpassing vertex in frontal view; median clypeal carina frequently present; body sculpture densely striate; small pit frequently situated medianly on weakly impressed promesonotal suture; metasternal process slender to acicular; row of stout setae on base of foretarsus opposite strigil present; petiolar node with no anterior peduncle; metacoxae and propodeum unarmed. All three members of the group are large species. This group is nevertheless heterogeneous and its three members were considered individually in the matrix.

VI. *minuta* group: head subquadrate; frontal carinae broadly expanded laterad; row of stout setae on base of foretarsus opposite strigil present; petiolar spiracles facing directly ventrad and sunken within a pit.

Phylogenetics.—The possible evolutionary history of the six species groups is depicted in Fig. 19. Fig. 19 was computed by the "ie-" option of Hennig '86. Figure 20 is a nelsen consensus tree calculated from 13 trees generated by the "ie" option of Hennig '86.

The *striatula* group subgroups are considered a sister group to the rest of the *Gnamptogenys* species considered. The *sulcata* and *mordax* groups are the most derived and are considered sister groups.



Figs. 19–20. Cladograms generated from the data in Table 1 by Hennig '86. 19, most parsimonious tree found by the "ie-" option, length 51, ci 58. 20, Nelsen consensus tree generated from the 13 most parsimonious trees found by the "ie" option, length 51, ci 58.

These results closely parallel Kugler's (1991) findings based upon the sting apparatus of several *Gnamptogenys* species. Within each of these groups we find species that apparently represent the transition from *striatula*-like ancestors and thus give additional support to the program results: the *hartmani* complexes of the *mordax* group, and the *volcano* and *fernandezi* complexes of the *sulcata* group. The *rastrata* group is probably closer to the *striatula* group than to the *mordax* or *sulcata* groups on account of characters such as triangular mandibles, long and usually sculptured scapes, the convex clypeal lamella of the *bispinosa* complex and the well developed

metacoxal tooth. The consensus tree recognizes two major groupings within the genus: *striatula*, and the rest. The "rest" make up a six-branched polytomy. Clearly further studies will be needed in the future in order to gain a better picture of the phylogenetic history of *Gnamptogenys*.

The *concinna* group is probably not monophyletic. It is diverse in mandibular shape, and in other details such as the development of the clypeal lamella or median clypeal carina. These traits as well as vestigial promesonotal suture are unusual remnants of plesiomorphies when compared with most other members of the genus. *G. haenschi* retains more plesiomor-

phies than the other two species and could be considered closer to the rootstock of the group. All are apparently specialized, either in feeding or nesting habits. This group opens a number of questions which can not be answered to satisfaction at present. Are the unarmed metacoxae plesiomorphic or apomorphic for this group? Could they represent relicts of an otherwise extinct lineage (or lineages) in *Gnamptogenys* history? Interesting parallels can be found in the shallow areolate ground sculpture and well-developed vertexal lobes of *minuta* subgroup members and those of several Old World species groups. A comparative study with Old World species could shed new light on the phylogeny of the genus. The striate sculpture of the *concinna* group can also be found, in a lesser degree, in the *simulans* complex.

The origins of Ectatommini can be traced to the late Cretaceous to early Tertiary, at least after the separation of Africa from Gondwana (80–90 Ma), but before the separation of South America from Paleontarctica (36–41 Ma) (Lattke 1994). Given the presence of *Gnamptogenys* in the Indomalaysian Region and their absence in Africa, the origin of the genus also extends at least to this time period and geographically could be related to southern South America -Paleontarctica. The spread of the ancestral fauna from South America to Central America probably took place during the mid Tertiary (30–38 Ma) as the Panama land bridge developed. Chances for an earlier exchange through possible connections between parts of the Greater Antilles and South America could have existed during the late Cretaceous (Donnelly 1988:26), but the geological history of the Caribbean region is still fraught with controversy (Rull 1989). The *mordax* group fossils from Dominican Amber show that by the late Oligocene to early Miocene (15–25 Ma), diversification of the American *Gnamptogenys* fauna was well underway. Potential ter-

restrial connections between Central America and the Greater Antilles could have existed during the Cenozoic via the presently submerged Nicaraguan rise which lays between Honduras and Jamaica (Donnelly 1988:28). It offered possibilities for dispersal until its subsidence during the middle Cenozoic. The presence of the Hispaniolan endemic species *G. haytiana*, *G. schmitti*, and *G. semiferox* lend support to such a connection and to the diversification of *Gnamptogenys* lineages some 26–34 Ma.

Ecology.—The ecology of *Gnamptogenys* found in Venezuela is treated in Lattke (1990) and should be consulted for more information. With the exception of a few additional tidbits of information little is added here. Generally most species are dwellers of mesic, forested habitats from Texas and Louisiana to northern Argentina. Nests are generally constructed in decomposing wood on the ground and tend to be small, rarely exceeding 500 adults. A few species exhibit polygyny.

The *striatula* group species are mostly generalist predators, but other species groups have developed varying degrees of specialization. This is taken to an extreme by the *rastrata* group species which prey only on certain diplopods. Beetles are the favorite of many members of other groups, and some species such as *G. hartmanni* and *G. horni* have also become fond of other ants as prey.

New World *Gnamptogenys*: A Synonymic List

When type material of a determined species was personally studied a "T" follows the distribution, plus the acronym of the collection where the specimen is deposited. Type material, in this case, includes specimens labelled either holotype, paratype, cotype, type series, or syntype.

acuminata Emery 1869. Tropical S. America.
acuta (Brown 1957a). Colombia–Bolivia. T:MCZC
alfaroi Emery 1894. Costa Rica–Ecuador
annomphila Lattke 1990. se Venezuela. T:MIZA

- andina* Lattke new sp. sw Colombia–Ecuador.
annulata Mayr 1887. Costa Rica–tropical S. America.
banksi (Wheeler 1930). Panama–Ecuador. T:MCZC
bispinosa (Emery 1890). Costa Rica–Colombia.
bisulca Kempf y Brown 1968. Costa Rica–Ecuador. T:MCZC
bufonis (Mann 1926). s Mexico–Nicaragua.
boliviensis Lattke, new species. n Bolivia.
bruchii (Santschi 1922). Argentina. T:MCZC
brunnea Lattke, new species. nw Colombia.
caelata Kempf 1967. Colombia–se Brazil.
= *soror* Kempf and Brown 1968
concinna (F. Smith 1858). Mexico–tropical S. America. T:BMNH
= *romani* Wheeler 1923.
= *semicircularis* Borgmeier 1929.
= *conica* Borgmeier 1929.
continua Mayr 1887 Mexico–tropical S. America.
= *panamensis* Santschi 1931
= *exarata* Emery, 1901. new synonymy.
cuneiforma Lattke, new species. Panama.
curvolyptea Lattke 1990. Colombia–Venezuela. T:MCZC
ejuncida Lattke, new species. s Colombia.
ericae Forel 1912, revalidated. n S. America.
= *bufonum* Weber 1938, new synonymy.
extra Lattke, new species. Colombia–Ecuador.
falcifera Kempf 1967. n S. America.
fernandezi Lattke 1990. Colombia–Ecuador. T:MIZA
fieldi Lattke 1990. n central Venezuela. T:MIZA
gentryi Lattke, new species. sw Colombia.
gracilis (Santschi 1929). Guiana Shield. T:MCZC
laticephala Lattke, new species. Ecuador.
haenschi Emery 1902. Costa Rica–tropical S. America.
hartmanni (Wheeler 1915). s United States–n S. America. T:MCZC
= *nigrifrons* Borgmeier, 1949. new synonymy. T:MUSP
= *turmalis* Kempf y Brown, 1968. new synonymy. T:MCZC
haytiana (Wheeler and Mann 1914). Hispaniola. T:MCZC
horni Santschi 1929. Panama–Bolivia. T:MCZC
ilimani Lattke, new species. Bolivian Andes.
ingeborgae Brown 1992. e Colombia. T:MCZC
interrupta Mayr 1887. Mexico–tropical S. America, Jamaica.
kempfi Lenko 1964. Brazil–Peru.
lanei Kempf 1960. Brazilian Amazonas.
levinates Baroni Urbani 1980. Dominican Amber.
lineolata Brown 1992. Hispaniola. T:MCZC
lucaris Kempf 1968. s Brazil.
mecotyle Brown 1958. Panama–tropical S. America. T:MCZC
mediatrix Brown 1958. Amazon drainage. T:MCZC
menozzi Borgmeier 1948. s Brazil. T:MUSP
= *schubarti* (Borgmeier, 1948) new synonymy. T:MUSP
mina (Brown 1957). w S. America. T:MCZC
minuta (Emery 1896). Belize–Brazil.
= *bufonis* (Mann 1922)
= *emeryi* (Forel 1901)
= *scabrosus* (Mann 1922)
= *mus* (Santschi 1931)
= *panamensis* (Weber 1940)
= *carinata* (Weber 1940)
= *pneodonax* Kempf 1968
moelleri (Forel 1912). Tropical S. America.
= *splendens* (Santschi 1929)
= *concinna* (Santschi 1929)
= *teffensis* (Santschi 1929) new synonymy. T:MCZC
mordax (F. Smith 1858). Mexico–tropical S. America. T:BMNH
= *nodosa* (Latreille 1802)
= *purensis* Forel 1912
= *sebastiani* Borgmeier 1937
nana Kempf 1960. Brazil.
nigrivittata Lattke, new species. sw Colombia.
perspicax Kempf and Brown 1970. Colombia–Ecuador. T:MCZC
petiscapa Lattke 1990. ne Venezuela. T:MIZA
pilosa Lattke, new species. sw Colombia.
pittieri Lattke 1990. n Central Venezuela. T:MIZA
pleurodon (Emery 1896). Tropical S. America.
= *emeryi* (Santschi 1929).
= *vidua* (Santschi 1929).
porcata (Emery 1896). Honduras–Bolivia.
= *magnifica* (Santschi 1921). new synonymy.
pristina Baroni Urbani 1980. Dominican Amber.
rastrata (Mayr 1866). s Brazil.
= *trigona* Emery 1905. new synonymy.
regularis Mayr 1870. Mexico–Paraguay.
= *splendida* Pergande 1895. T:CASC
= *fiebrigi* Forel 1909.
= *arcuata* (Santschi 1929).
reichenspergi (Santschi 1929). Amazon–Orinoco drainage.
relicta (Mann 1916). Amazon–Orinoco drainage. T:USNM
rimulosa (Roger 1861). s Brazil.
schmitti (Forel 1901). Hispaniola.
= *minor* (Wheeler 1936). T:MCZC
semiferox Brown 1958. Hispaniola. T:MCZC
siapensis Lattke, new species. s. Venezuela.
simulans (Emery 1896). Costa Rica. T:USNM
stellae Lattke, new species. Costa Rica.
striatula Mayr 1883. Mexico–Argentina, Caribbean. T:BMNH
= *curtula* (Emery 1896) new synonymy.
= *stolli* (Forel 1899) new synonymy.
= *brasiliensis* (Emery, 1902).
= *angustiloba* (Forel 1908).
= *paulina* (Forel 1908).
= *simplicoides* (Forel 1908) new synonymy.
= *pernambucana* (Santschi 1929).
= *calcarata* (Santschi 1929).

- = *antillana* (Santschi 1929). T:MCZC
- = *hybrida* (Santschi 1929).
- = *mayri* (Santschi 1929).
- = *isthunica* (Santschi 1929).
- = *recta* (Santschi 1929). T:USNM
- = *rustica* (Santschi 1929) new synonymy.
- = *wheeleri* (Santschi 1929) new synonymy. T:MCZC
- = *arcuata* (Santschi 1929) new synonymy.
- = *wasmanni* (Santschi 1929) new synonymy.
- striolata* (Borgmeier 1957). se Brazil. T:MUSP
- strigata* (Norton 1871). Mexico–Colombia.
- = *simplex* (Emery 1896).
- sulcata* (F. Smith 1858). Mexico–tropical S. America. T: BMNH
- = *tornata* (Roger 1861). new synonymy.
- = *lineata* Mayr 1870.
- = *cearensis* Forel 1912.
- = *nitens* Mann 1916. T:USNM
- = *ypiraugensis* Borgmeier 1928.
- tortuolosa* (F. Smith 1858). Amazon–Orinoco drainage. T:BMNH
- = *quitensis* Forel 1920.
- transversa* Lattke, new species. Panama.
- triangularis* Mayr 1887. Panama–Argentina; se United States.
- = *richteri* (Forel 1920)
- = *aculeaticoxae* (Santschi 1921) new synonymy.
- volcano* Lattke, new species. Costa Rica.
- vriesi* Brandao & Lattke, 1990. Ecuador.

KEY TO THE WORKERS OF THE NEW WORLD SPECIES OF GNAMPTOGENYS.

Note: In some species the difference between the promesonotal suture and the metanotal groove may be hard to establish when only one of the two is present, which is the usual case. In a dorsal view the lateral margins of the pronotum converge posterad and at the end of the convergence, when the margins more or less straighten out, the promesonotal suture is usually slightly arched anteriorly, while the metanotal groove is usually straight.

- 1. Petiolar spiracle directed ventrally and within a depression *minuta* group (see Lattke 1991)
 - Petiolar spiracle directed anteroventrally and not depressed; Pronotum separated from mesonotum by very distinct suture which completely cuts dorsal sculpture 2
 - Petiolar spiracle directed ventrolaterally and not depressed; Promesonotal suture absent to well impressed, but never completely cuts sculpture 23
- 2. Petiolar in lateral view with subparallel anterior and posterior margins sharply set off at right angles to relatively brief dorsal margin (Fig. 21); vertex usually smooth and shining, occasionally with weak transverse triae 3
 - Petiole not as above, in lateral view with anterior margin either broadly curving into dorsal margin or separated by broad angle (Figs. 22–4, 46, 49, 52); vertex strongly sculptured 6
- 3. Mesosomal dorsum with extensive smooth and shining areas 4
 - Mesosomal dorsum totally sculptured, usually rugulose or costulate 5
- 4. Metanotal groove well impressed, breaking sculpture; metacoxae armed; anterolateral lobes on declivitous propodeal face lacking (Amazon–Orinoco drainage) *relictata*
 - Metanotal groove absent; metacoxae unarmed; small lobes present on anterolateral declivitous propodeal face (Amazon–Orinoco drainage) *reichenspergi*
- 5. Postpetiolar dorsum transversely rugulose; body color yellowish (Hispaniola) *haytiana*
 - Postpetiolar dorsum longitudinally costulate; black to dark brown (w South America) *mina*
- 6. Mesosomal dorsum with well developed metanotal groove 7
 - Metanotal groove absent 9
- 7. Dorsum of gastric tergites I and II smooth and shining (sw Colombia) *gentryi* n. sp.
 - Dorsum of gaster with longitudinal costulae 8
- 8. Subpetiolar process subquadrate, with posterior angle (Fig. 21; Costa Rica to Ecuador, Andes) *bisulca*
 - Subpetiolar process shaped as an anteriorly projecting lobe with no posterior angle Fig. 42) (nw Colombia) *brunnea* n. sp.
- 9. Petiolar node in lateral view relatively erect, posterodorsal and anterodorsal angles not differing notably (Fig. 22) 10
 - Petiole in lateral view posteriorly inclined, anterior margin joins dorsal margin through broad convexity that contrasts with sharp angle between posterior and dorsal margins (Figs. 23, 24, 46, 49, 52) 12

10. SL < 1.08 mm 11
 - SL > 1.08 mm (tropical S. America) *moelleri*
11. Declivitous propodeal face with 5–11 longitudinal costulae between spiracles and 1–3 transverse costulae between each spiracle and longitudinal costulae (Fig. 26); decumbent pubescence on scapes sparse, < six decumbent and suberect hairs (Mexico to Argentina, Caribbean) *striatula*
 - Declivitous face with 13–16 longitudinal costulae between spiracles and no transverse costulae between each spiracle and longitudinal costulae (Fig. 25); scapes with dense and uniform decumbent pubescence, 1–3 subdecumbent hairs (se Venezuela) *ammophila*
12. Posterodorsal angle of petiolar node forms a sharp to bluntly pointed apex that overhangs posterior margin (Figs. 23, 24, 46, 49, 52); subpetiolar process in ventral view with uniformly narrow ventral edge, posteriorly widening only at junction with node (Fig. 29) 13
 - Petiolar node not, or slightly overhanging posterior margin (Figs. 40, 57); subpetiolar process in ventral view with cuneiform ventral edge: anteriorly thin, wider posterad with bifurcate apex that forms posterior angle of subquadrate process (Fig. 30) 20
13. Petiolar node with a blunt posterodorsal apex (Figs. 24, 46, 49, 52) 14
 - Petiolar node with acute posterodorsal point (Fig. 23; Colombia to Bolivia) *acuta*
14. Postpetiolar sternum totally costulate or striate; vertex usually with one (occasionally up to 3) transverse costulae next to vertexal carinae 15
 - Postpetiolar sternum with a basal median smooth and shining area; vertex with 4–5 transverse costulae next to vertexal carinae (Guiana Shield) *gracilis*
15. SSC < 10 (Fig. 27) 18
 - SSC > 10 (Fig. 28) 16
16. Body and legs brown, sculpture costulate to striate; body with abundant decumbent pubescence; subpetiolar process lobiform and without acute projection 17
 - Body piceous and legs ferruginous; body with abundant pubescence; subpetiolar process usually with an acute anteroventral projection, sometimes blunt, especially in specimens from Central America (Honduras to Bolivia) *porcata*
17. Femora with abundant erect to suberect hairs; ventral surfaces of meso- and metacoxae with erect hairs; gastric sculpture striate (sw Colombia) *pilosa*, n. sp.
 - Femora with decumbent to subdecumbent hairs and few or no erect to suberect hairs; ventral surfaces of meso- and metacoxae without erect hairs; gastric sculpture costulate (s Colombia) *ejuncida*, n. sp.
18. Five or more standing hairs on scapes and tibiae 19
 - One or no suberect and subdecumbent hairs on scapes and tibiae (Colombia–Ecuador) *extra*, n. sp.
19. Declivitous propodeal face with transverse costulae; petiolar node with anterior peduncle (Fig. 24; tropical S. America) *pleurodon*
 - Declivitous propodeal face with longitudinal costulae; node without peduncle (Fig. 59; sw Colombia) *nigrivitre*a, n. sp.
20. Postpetiolar sternum with well defined costulae or striae; dorsal propodeal face not notably depressed below mesonotum, dorsal and declivitous faces confluent 21
 - Postpetiolar sternum with weak irregular rugae; in lateral view dorsal propodeal face separated from mesonotum by notable depression, dorsal and declivitous faces sharply separated by a ridge (n Central Venezuela) *pittieri*
21. Scapes with moderate to weak pubescence, five or more standing hairs present 22
 - Scapes with dense, white subdecumbent pubescence, 0–2 standing hairs present (Bolivian Andes) *ilimani* n. sp.
22. HW > 0.84, WL > 0.35; OI < 0.16 (sw Colombia–Ecuador) *andina*, n. sp.
 - HW < 0.84, WL < 0.35, OI > 0.16 (Mexico–Colombia) *strigata*
23. With head in frontal view antennal scapes barely or do not reach the vertexal margin, never beyond, when laid back as straight as possible from insertions 24
 - Scapes clearly reach beyond vertexal margin 38

| | |
|--|-----------------------------|
| 24. Mandibular dorsum with continuous striae or costulae over the basal one-fourth or more of length | 25 |
| – Mandibular dorsum entirely smooth and shining, sometimes with scattered punctures | 27 |
| 25. Distinct median carinae visible on clypeus; eyes small, $OI < 0.1$; mandibular dorsum entirely and densely striate (Costa Rica–tropical S. America) | <i>haenschi</i> |
| – No distinct median carinae on clypeus; eyes larger, $OI > 0.2$; mandibular dorsum without dense striae | 26 |
| 26. Mandibular dorsum with costulae on basal one fourth or less, rest smooth and shining; propodeal declivity with longitudinal costulae (s United States–n South America) | <i>hartmani</i> (in part) |
| – Mandibular dorsum mostly rugulose; propodeal declivity with transverse costulae | <i>transversa</i> n. sp. |
| 27. Propodeal dorsum mostly transversely striate | 28 |
| – Propodeal dorsum mostly longitudinally costulate or striate, continuous with rest of notal sculpturing | 30 |
| 28. Head subquadrate, $CI > 0.78$; body brown to dark brown | 29 |
| – Head notably rectangular and elongate, $CI < 0.78$; body black (Costa Rica–Ecuador) | <i>alfaroi</i> |
| 29. Costulae on mesosomal and petiolar dorsum subopaque; propodeum with small teeth; metacoxal teeth (Brazil and Peru) | <i>kempfi</i> |
| – Very fine striae on mesosoma and node; no teeth on propodeum nor on metacoxae (Costa Rica to tropical S. America) | <i>annulata</i> |
| 30. Clypeal lamella medianly straight and laterally acutely angulose; subpetiolar process subquadrate, usually with acute posteroventral tooth | 36 |
| – Clypeal lamella usually concave and laterally rounded, never acutely angular (rarely with slight median projection and laterally bluntly angular); subpetiolar process usually projecting anteriorly as subtriangular lobe, sometimes subquadrate, but never with acute posteroventral tooth | 31 |
| 32. Mandibles subtriangular to subfalcate; metanotal groove well-impressed | 32 |
| – Mandibles triangular; metanotal groove absent (Brazil) | <i>nana</i> |
| 32. Metacoxa with dorsobasal lobe or tooth | 34 |
| – Metacoxa lacking tooth or lobe, at most small swelling or low tubercle present | 33 |
| 33. Body sculpture striate; gastric tergum 2 smooth and shining; clypeal lamella laterally bluntly angulose, slightly projecting anterad medianly and with small concavity in middle of projection (Fig. 60; Costa Rica) | <i>stellae</i> n. sp. |
| – Body sculpture costulate; gastric tergum 2 longitudinally costulate; clypeal lamella laterally rounded and medianly concave (Fig. 43; Mexico to tropical S. America, Jamaica) | <i>interrupta</i> |
| 34. Metacoxal dorsum with low triangular lobe; $HW < 1.12$, $WL < 1.81$ mm | 35 |
| – Metacoxal dorsum with high, approximately parallel-sided lobe or tooth; HW usually > 1.12 , $WL > 1.81$ mm (Mexico to tropical S. America) | <i>mordax</i> |
| 35. Cephalic dorsum striate; anterolateral lobes of declivitous propodeal face weakly developed (n Bolivia) | <i>boliviensis</i> , n. sp. |
| – Cephalic dorsum costulate; anterolateral propodeal lobes well developed (Mexico to tropical S. America) | <i>continua</i> |
| 36. Metanotal groove weakly impressed, visible only with limited angles of view; subpetiolar process with acute posteroventral tooth; anterolateral angles of declivitous propodeal face bordered by raised carinae that cross over costulate sculpture | 37 |
| – Metanotal groove well-impressed, visible with any angle of view; subpetiolar process without acute posterior tooth; declivitous propodeal face lacking carinae different from costulate sculpture (s. Brazil) | <i>rimulosa</i> |
| 37. Declivitous propodeal face with longitudinal costulae that converge posterad; anterior nodal face with transverse costulae; meso-metapleural suture absent or very weakly impressed (Panama to Bolivia) | <i>horni</i> |

- Declivitous propodeal face with longitudinal parallel costulae; anterior nodal face mostly longitudinally costulate, basal transverse costulae frequently present and rarely occupy all; meso-metapleural suture distinctly impressed (Mexico to Paraguay) *regularis*
- 38. Mandibles very elongate: falcate or subfalcate, only their apices touching or crossing when closed (Figs. 35, 54) 39
- Mandibles triangular or subtriangular, apical and basal margins separated by rounded or angular basal angle (Figs. 33–34, 36–37) 43
- 39. Declivitous propodeal face with spines or denticles; metacoxal tooth present 40
- Declivitous propodeal face rounded, no trace of spines or denticles; coxal tooth absent 42
- 40. Inner basal mandibular border with short triangular tooth that represents basal angle (Fig. 54) 41
- Inner basal mandibular border with broadly convex lobe or flange (Amazon drainage) *mediatrix*
- 41. Clypeus with two lobes between antennal fossae and anterior lamella, lobe protrude over lamella in front view; mesothoracic spiracles not set in deep depressions (Ecuador) .. *laticephala*, n. sp.
- Clypeus without lobes between antennal fossae and anterior lamella; spiracles of mesothorax set in deep depressions (Panama to Ecuador) *banksi*
- 42. Mandibles long and slender (Fig. 36); dorsal propodeal face evenly and transversely costulate (Hispaniola) *schmitti*
- Mandibles shorter and wider; dorsal propodeal face subvermiculately and longitudinally costulate (Hispaniola) *semiferox*
- 43. Mandibles mostly smooth and shining, with scattered punctures, subtriangular to triangular, sometimes striae or costulae present on basal one-third or less; usually without transverse sutures on mesosomal dorsum (except *concinna*) 44
- Mandibles with longitudinal rugulae or striae (sometimes weakly impressed), always triangular, never subtriangular; metanotal suture distinctly impressed 55
- 44. HW > 1.43; WL > 2.27 mm 45
- HW < 1.43; WL < 2.27 mm 46
- 45. Sculpture costulate; metacoxae with dorsal tooth; petiolar node ends in blunt angle; black (Amazon–Orinoco drainage) *tortuolosa*
- Sculpture striate; metacoxae without dorsal tooth, with low tubercle at most; petiole ends in acute point or beak; ferruginous (Mexico to tropical S. America) *concinna*
- 46. Sculpture striate; anterolateral corners of declivitous propodeal face bordered by carinae that cross costulae; antennal scape when laid back does not surpass vertexal margin by more than one apical width 47
- Sculpture costate; declivitous propodeal face without carinae distinct from costae; scapes surpass vertexal margin by more than an apical width 48
- 47. Posterior face of petiolar node longitudinally costulate (s United States to n S. America) *hartmani* (in part)
- Posterior nodal face transversely costulate (Argentina) *bruchi*
- 48. Posterior face of petiolar node transversely costulate 49
- Posterior face of node longitudinally costulate 51
- 49. Anterior clypeal lamella laterally acutely angular; mandibles subtriangular, basal and apical margins joined by very broad continuous convexity (Fig. 34) 50
- Clypeal lamella very evenly convex laterad; mandibles triangular, basal and apical margins separated by angle (Fig. 33; Venezuela to Ecuador) *fernandezi*
- 50. Petiolar node with posterior pointed projection; declivitous propodeal face with longitudinal costulae; body color uniformly brown (tropical S. America) *acuminata*
- Node sometimes with slight posterior projection, but never pointed; declivitous propodeal face with transverse costulae, rarely longitudinal; color variable, usually with brown and ferruginous areas, rarely totally brown (Mexico to tropical S. America) *sulcata*
- 51. Anterior clypeal lamella laterally acutely angulate 52

- Clypeal lamella laterally rounded or obtusely angulate 53
- 52. HW < 1.11, WL < 1.72 mm; anterior clypeal lamella straight (Fig. 31; n S. America) ... *ericae* reval. sp.
- HW > 1.11, WL > 1.72 mm; anterior clypeal lamella medially convex and laterally concave (Fig. 32; Venezuela and Colombia) *curvoclypeata*
- 53. Declivitous propodeal face with longitudinal costae; clypeal lamella straight anterad and laterally rounded; mandibles subtriangular, basal and apical margins meeting through broad convexity (Fig. 62) 54
- Declivitous propodeal face with transverse costae; clypeal lamella excised mesad and with two lateral convexities; mandibles roughly triangular, apical and basal margins separated by notch (Fig. 64; Costa Rica) *volcano*, n. sp.
- 54. Petiolar node with dorsal margin more or less evenly convex in lateral view; metacoxal tooth denticle-like; subpetiolar process with acutely pointed angles (s Brazil) *lucaris*
- Petiolar node with dorsal surface flat; metacoxal tooth broadly triangular; subpetiolar process bluntly angulate (s Venezuela) *siapensis*, n. sp.
- 55. Antennal scapes usually smooth and shining 56
- Scares with longitudinal striae or rugulae (sometimes partially effaced) 60
- 56. Scares surpass vertexal margin by two or more apical widths; HW > 1.07, WL > 1.64 mm 59
- Scares when laid back do not surpass vertexal margin by more than one apical width; HW < 1.07, WL < 1.64 mm 57
- 57. Body sculpture striate; no propodeal denticles; ventral petiolar process in lateral view projecting anterad as a lobe, lacking a posterior angle; Hispaniola Island *lineolata*
- Sculpturing costulate; propodeal denticles present; petiolar ventral process with a pointed posterior corner; South America 58
- 58. Costulae on dorsum of metanotum and propodeum well defined; petiole in dorsal view with concentric costulae (s Brazil) *rastrata*
- Costulae on dorsum of metanotum and propodeum mostly effaced; petiole in dorsal view transversely costulate (e Colombia) *ingeborgae*
- 59. Propodeal teeth longer than diameter of propodeal spiracles; petiolar node longer than wide and subpetiolar process projects anterad as triangular lobe (Brazilian Amazon drainage) *lanei*
- Propodeal teeth shorter than diameter of propodeal spiracles; petiolar node wider than long; subpetiolar process subquadrate (s Brazil) *menozzi*
- 60. Anterior pronotal margins with at least five transverse costulae or rugulae; eyes prominent and bulging (Fig. 37) 61
- Anterior pronotal margin with longitudinal costulae that extend caudad across rest of mesosomal dorsum; eyes not bulging and prominent, relatively flat (Fig. 38; Florida, Panama to Argentina) *triangularis*
- 61. Vertex with 4-5 transverse costulae; anterior one-half of postpetiolar tergum rugose ... 62
- Vertex with longitudinal costulae; anterior one-half of postpetiolar tergum longitudinally costulate 63
- 62. Dorsum of metanotum and all of propodeum with transverse costulae (Panama) *cuneiforma* n. sp.
- Dorsum of metanotum and propodeum longitudinally costulate; declivitous propodeal face with weak longitudinal costulae, smooth and shining mesad (Panama to tropical S. America) *mecotyle*
- 63. Propodeal spines at least as long as distance between inner sides of their base (Fig. 12); ferruginous species (Costa Rica to Colombia) *bispinosa*
- Propodeal spines shorter (Fig. 13); black species (Colombia to Ecuador) *perspicax*

New World species of *Gnamptogenys*

In this section the species are arranged in alphabetical order. In the synonymy listings, when more than one citation follows a junior synonym, the first author, after the author of the species, is responsible for that synonymy. The diagnosis is meant to complement the results obtained in the key. In order to avoid repeating information already published the reader should consult Lattke (1990) for additional data concerning ecology and localities of species previously known from Venezuela. For the sake of brevity the dates and collector's names have been omitted.

Gnamptogenys acuminata Emery

Gnamptogenys acuminata Emery 1896:50; Brown 1958:228, 236, 299; Kempf 1961:491; Kempf 1972:111; Kempf 1976:51; Lattke 1990:9.

Diagnosis.—Mandibles subtriangular; longitudinal costulae on mesosoma and declivitous propodeal face; transverse sutures weak, visible only with certain angles of light; body dark brown to black; coxae and basal two-thirds of femora testaceous to brown-testaceous; tibiae, apex of femora, antenna and mandibles brown.

Ecology.—Found in humid forests, nesting in rotting wood.

Comments.—The acute posterior tooth

on the petiolar node, combined with longitudinal costulae on the declivitous propodeal face, seem to provide the most reliable distinction from *tornata*. Color in *acuminata* is not so variable but light-pigmented forms can occasionally be found. The mesometepisternal suture is usually absent.

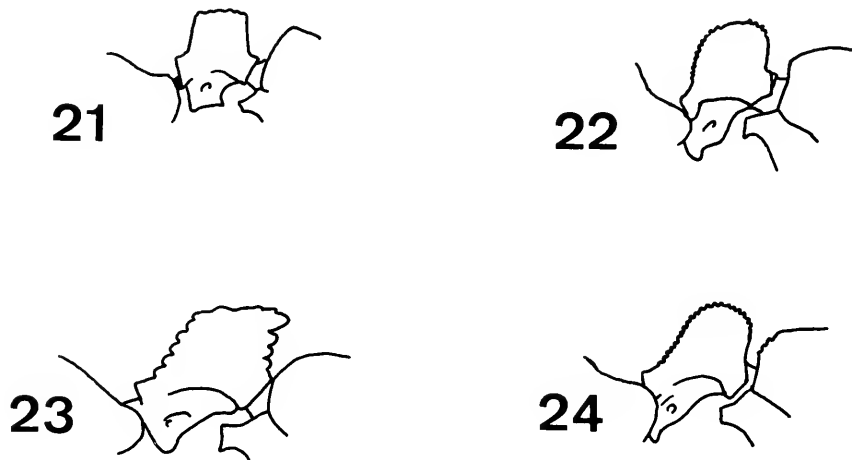
Specimens Examined.—BRAZIL, Amazonas: Ig. Marianil, Rio Branco Rd, 24 km NE Manuas. COLOMBIA, Meta: Caño EL Buque, S Villavicencio, 480 m. PERU, Loreto: 15 km WSW Yurimagua, 5°59'S 76°13'W, 220 m; Panguana: 9°37'N 74°56'W, 220 m. VENEZUELA, Bolívar: Rio Cuyuní, 66 km SSE El Dorado, 6° 09' N 61° 30'W, 250 m; 10 km E Icabarú, 700 m. Amazonas: Río Baria, 0°50'N 66°10'W, 140 m.

Gnamptogenys acuta Brown

Holcoponera acuta Brown 1957:491.

Gnamptogenys acuta (Brown); Brown 1958:300; Kempf 1972:111.

Diagnosis.—Similar to *striatula*; four to six transverse costulae on anterior pronotal face, rest of mesosoma with longitudinal costulae; longitudinal costulae on anterior face of postpetiole; body dark brown to black, legs brown.



Figs. 21–24. Lateral view of petiole. 21, *G. relictata*; 22, *G. moelleri*; 23, *G. acuta*; 24, *G. pleurodon*.



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27



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Figs. 25–26. View of declivitous propodeal face. 25, *G. ammophila*; 26, *G. striatula*.

Figs. 27–28. Frontal view of scapes, showing hairs and pilosity. 27, *G. pleurodon*; 28, *G. porcata*.

Ecology.—Found in low to premontane jungles.

Comments.—Not frequently collected, knowledge of its range has expanded slowly.

Specimens Examined.—ECUADOR, Napo: 2–8 miles N Puyo, Pastaza, 935 m; original locality unknown: Quarantine Station, San Pedro, California. PERU, Junín: Colonia Perene, Río Perene, 18 km NE La Merced; Loreto: Boquerón, 500 m; COLOMBIA, Meta, Mesetas, 780 m.

***Gnampptogenys alfaroi* Emery**

Gnampptogenys alfaroi Emery 1894:145; Brown 1958:301; Kempf 1972:111.

Diagnosis.—Mandibular dorsum smooth and shining with some punctulae; metacoxal spine present; subpetiolar process anteriorly projected; gastric tergum 2 with basal one-half longitudinally costulate, the rest smooth and shining; disk of postpetiolar sternum smooth and shining; body black; legs and antennae brown.

Ecology.—Known from montane rain forest.

Comments.—The Ecuador record extends its distribution from the only previously known localities in Costa Rica. This species is a striking member of the *mordax* group due to its elongated, almost cylindrical body. Its relationship with other members of the *mordax* group is not clear. It is rarely collected.

Specimens Examined.—COSTA RICA,

Turrialba. ECUADOR, Guayas: 3 km SW Bucay (MCZC).

***Gnampptogenys ammophila* Lattke**

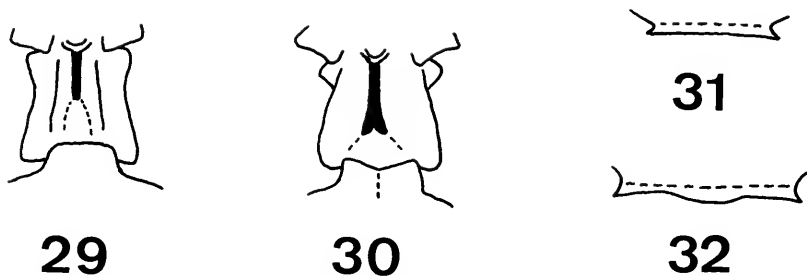
Gnampptogenys ammophila Lattke 1990:9.

Diagnosis.—Black, finely costulate with brown scapes and mandibles, light brown legs. Subpetiolar process subquadrate, not as projecting anterad as in *striatula*. Mesosomal dorsum with longitudinal costulae and erect hairs up to 0.30 mm in length.

Ecology.—This species is unique within the genus due to its savanna nest sites as opposed to the forest preferences of most species. Its range is apparently restricted to high (>1200m), cool savannas of the Upper Río Caroní watershed (La Gran Sabana). It has not been found in lower savannas, despite the fact that another ant, *Pogonomyrmex naegeli*, is widespread in savannas isolated in the midst of great expanses of forest. The extent of savannas in the Guiana Shield was much broader during the last glaciation (75,000–11,000 B.P.), as were generally cooler temperatures and a drier climate (Schubert 1988; Clapperton 1993). Such conditions could conceivably have favored the origin of this species from its apparent sister species *G. striatula* during the course of the last glaciation.

Comments.—See Lattke 1990.

Specimens Examined.—VENEZUELA, Bolívar: vía El Dorado–Santa Elena, km 141, Río Apanwao, 5°52'N 61°26'W, 1500 m.



Figs. 29–30. Ventral view of petiole showing shape of subpetiolar process (outlined in black). 29, *G. gracilis*; 30, *G. andina*.

Figs. 31–32. Frontal view of clypeal lamella. 31, *G. sulcata*; 32, *G. curvoclypeata*.

Gnampptogenys andina Lattke,
new species
(Figs. 39–40)

Type Specimens Examined.—Holotype worker. COLOMBIA, Valle: Parque Farallones de Cali, El Topacio, 20 km NW Cali, 76 37'N 2 30'W, 1550 m, 31-XII-1981, J. Lattke No. 220. Deposited in MIZA. Paratypes (all from Colombia, Valle): (1). 22 workers from the same nest series as the holotype. (2) 21 workers, same data as holotype except collection numbers 220, 214, 218. (3). 18 workers, Cali-Buenaventura road, km 21, 15 km NE Cali, 1300–200 m, 1-X-1975, J. Lattke, leg. (4). 6 workers, CVC station near Pance, 15 km W Cali, 1700 m, 12-XII-1975, J. Lattke, leg.

Additional Specimens (not paratypes).—ECUADOR, Bolívar, 20 km de Palzabamba, 1500–1800 m, 18-XI-87, N. Zavala, leg. Six paratypes deposited in MCZC and three in each of the following: LACM, BMNH, CASC, MUSP. The remainder of paratypes and other specimens deposited in MIZA.

Worker.—Holotype (Paratypes) measurements: HL 1.04 (1.02–1.08); ML 0.40 (0.26–0.36); HW 0.88 (0.82–0.94); SL 0.86 (0.86–0.92); ED 0.12 (0.10–0.14); WL 1.36 (1.36–1.60) mm; CI 0.85 (0.83–0.90); SI 0.98 (0.93–1.10); OI 0.14 (0.11–0.17) $n=7$.

Typical *striatula* group member: Roughly costulate sculpture. Vertexal margin concave in frontal view; clypeal costulae extend slightly onto anterior lamella; man-

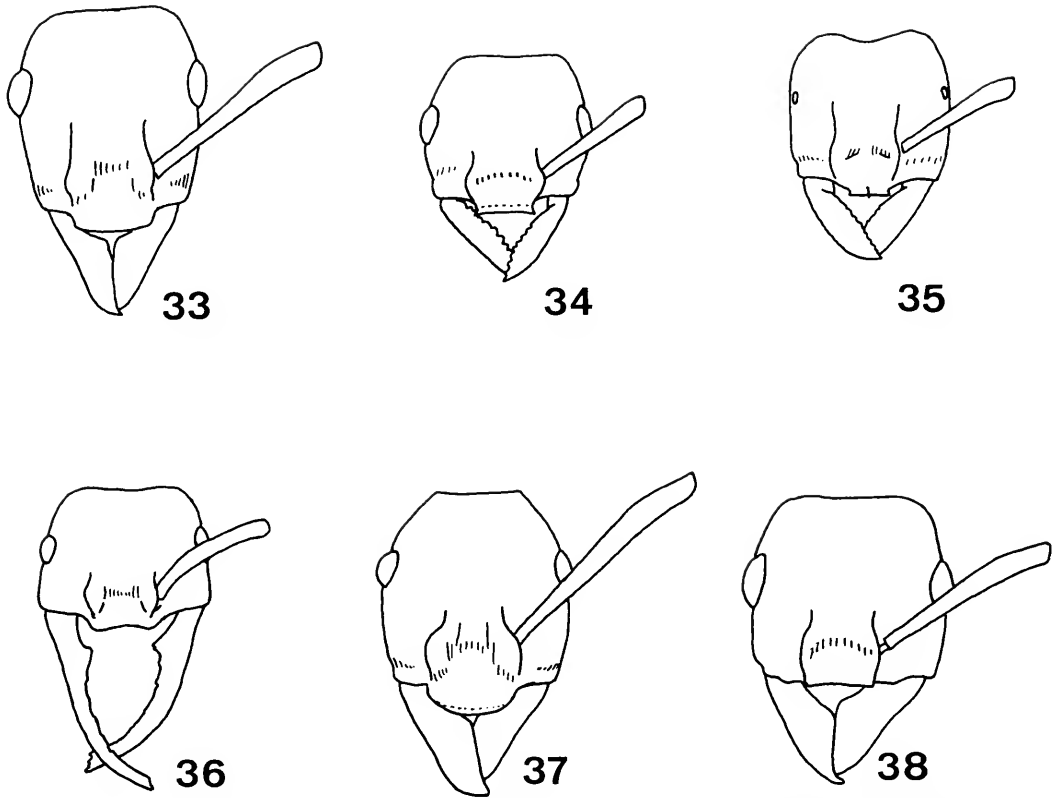
dibles triangular and mostly striate except for smooth and shining lamellate basal corner and margin of chewing border; compound eyes relatively small; in lateral view dorsal propodeal margin not notably depressed below rest of mesosomal dorsum; propodeal spiracle slightly elevated above rest of sculpture and at edge of declivitous surface; petiolar node posteriorly inclined; subpetiolar process subquadrate, typical of *strigata* subgroup. Longitudinal costulae present on declivitous postpetiolar face. Weak transverse costulae on postpetiolar ventrum.

Fairly abundant standing hairs on body, but very sparse appressed pubescence. Legs smooth and shining, except for numerous piligerous punctures. Metacoxal dorsum with a well-developed denticle. Body dark brown to black with yellowish legs.

Male.—Longitudinal costulae on cephalic dorsum; mandibles triangular and costulate; pronotum smooth and shining with piligerous punctures; pronotum with piligerous punctures; mesonotum mostly smooth and shining except for narrow anterior band of transverse striae; declivitous propodeal face with longitudinal rugulae that do not reach anterior dorsal face; gaster smooth and shining.

Queen.—Unknown.

Discussion.—This species is near *strigata* and though the differences are not striking, they seem consistent enough to define a



Figs. 33–38. Frontal view of head. 33, *G. fernandezi*; 34, *G. sulcata*; 35, *G. haenschii*; 36, *G. schmitti*; 37, *G. bispinosa*; 38, *G. triangularis*.

species. *G. strigata* is smaller (HW 0.74–0.80; WL 1.20–1.34 mm), with relatively larger eyes (OI 0.17–0.20) and shorter scapes (0.70–0.78 mm) and dorsal propodeal face in lateral view is usually depressed below the rest of the mesosomal dorsum. It is probably sympatric with *andina* in part of its range, having been found only 51 km away from the *andina* type locality. The male of *strigata* has a median area of rugosity on the mesonotum and totally rugulose propodeum. Individuals of the Ecuadorean sample are slightly larger than the Colombian specimens.

Etymology.—The name alludes to the Andes, a portion of which is inhabited by this species.

Gnamptogenys annulata Mayr

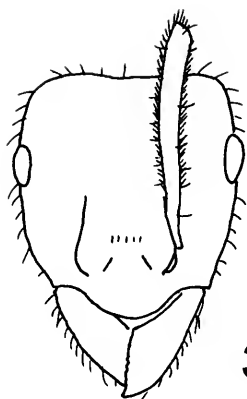
Ectatomma (*Gnamptogenys*) *rimulosa* var. *annulata* May 1887:543.

Ectatomma (*Gnamptogenys*) *annulatum* Mayr; Mann 1916:408; Luederwalt 1926:23.

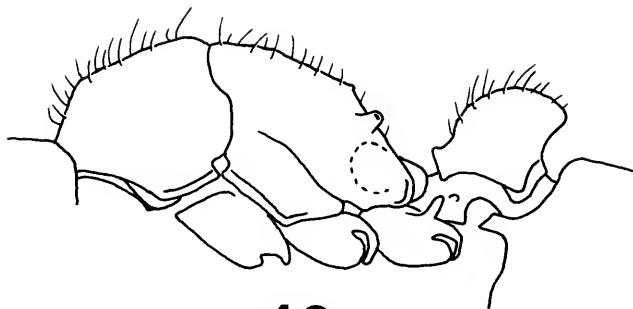
Gnamptogenys annulatum Mayr; Mann 1922:3; Brown 1958:300; Kempf 1960:390; Kempf 1961:491; Kempf 1969:275; Kempf 1972:112; Kempf 1976:51; Lattke 1990:11.

Diagnosis.—Finely striate species; longitudinal striae on head, promesonotum and gastric segments 2 and 3; petiolar dorsum with transversely arched striae; mandibles subtriangular; metacoxal spine absent; body reddish brown; coxae ferruginous yellow; tibiae and femora yellow to testaceous but apically ferruginous yellow to ferruginous.

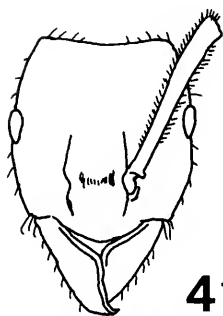
Ecology.—J. Longino (pers. comm.) reports from a nest midden chitinous fragments of Coleoptera, aradid bug nymphs, an unidentified male ant, and a *Camponotus* worker. An apparently recently killed



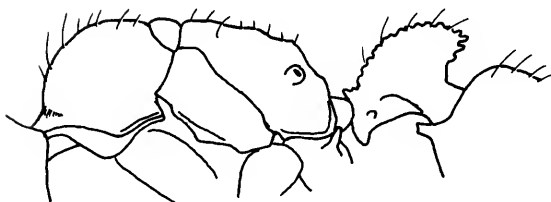
39



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Figs. 39–42. Frontal view of head, and lateral view of mesosoma and petiole. 39–40, *G. andina*; 41–42, *G. brunnea*.

Pheidole (cephalica?) queen was also found in a nest chamber.

Comments.—The gauge of costulation can vary from striate to finely costulate, but coloration is fairly stable.

SPECIMENS EXAMINED: BOLIVIA, Caranaví: vic. Radio, 800 m. BRAZIL, Amazonas: 80 km NNE Manaus, 2°25'S 59°46'W, 80 m. COLOMBIA, Valle: Bajo Calima; Cauca: Isla La Gorgona. COSTA RICA, vic. Guapiles, Río Toro Amarillo; Prto. Limón; Limón: Tortuguero, < 100m, 10°35'N 83°31'W; Heredia: 10°20'N 84°84'W, 500 m; 3 km S Puerto Viejo, 10°26'N 84°00'N, 50 m; Pq. Nac. Braulio Carrillo, Carrillo, 500 m; Península de Osa, Sirena, 8°28'N 83°35'W; Alajuela: Río Peñas Blancas, 10°19'N 84°43'W, 800 m. EC-UADOR, Pichincha: 6 km W Sto. Domingo

de los Colorados, 953 m; Maquipucuna, 5 km ESE Nanegal, 0°70'N 78°38'W, 1250m; Sucua. GUIANA, Kartabo. PERU, Panguana: 9°37'S 74°56'W, 220 m; Tingo María: Valle de Monsón; Madre de Dios: Res. Río Tambopata, 30 km SW Prto. Maldonado, 290 m; Loreto: Boquerón, 500m; San Martín: Davidcillo, 30 km NNE Tarapoto, 6°15'S 76°15'W. VENEZUELA, Táchira: Uribante-Caparo, Las Cuevas, 7°47'N 71°46'W, 500 m; Barinas: Ticoporo, 8°04'N 70°48'W, 250 m; Amazonas: Alto Mavaca, 2°01'N 65°07'W, 200 m; Alto Siapa, 1°42'N 64°38'W, 500 m.

***Gnamptogenys banksi* (Wheeler)**

Emeryella banksi Wheeler 1930:10.

Gnamptogenys banksi (Wheeler); Brown 1958: 227,233; Kempf 1972:112.

Diagnosis.—Finely costulate; head broad with longitudinally striated scapes; meso-metanotal suture not deeply impressed, but distinct. It lacks the long, fine mandibular sulcus present in *laticephala*.

Ecology.—Found in rotten logs in lowland rain forest, this species is a specialist millipede predator.

Comments.—It is rarely collected. A specimen from Barro Colorado has two deep fossae on the posterolateral margin of the mesonotum. The type was examined.

Specimens Examined.—ECUADOR, Guayas: 3 km S Bucay. PANAMA, Isla Barro Colorado (MCZC).

Gnamptogenys bispinosa (Emery)

Ectatomma (Poneracantha) bispinosum Emery 1897:547.

Ectatomma (Holcaponera) bispinosum Emery; Emery 1890:40.

Holcaponera bispinosa (Emery); Wheeler 1952: 132–133.

Gnamptogenys bispinosa (Emery); Brown 1958: 301; Kempf and Brown 1970:319; Kempf 1972:112.

Diagnosis.—Eyes subglobulose, scapes long and surpassing vertexal margin; mandibles edentate. Promesonotal suture breaks sculpture dorsally but not laterally; mesometanotal suture deep and broad. Head, mesosoma and postpetiole rugose; ferruginous.

Ecology.—This wet forest species is a millipede specialist. J. Longino (pers. comm.) observed the following two raids from the same colony, both at 11:00 AM: "A column of 20 workers was moving along a liana on the forest floor. They left the liana and moved very slowly across the leaf litter, frequently bunching up. They all went under a leaf and then agitated ants could be seen coming out from under the leaf, 2 or 3 ants at a time, cleaning their antennae and mandibles. I removed the leaf to find the ants attacking a millipede. Some were stinging and some were pulling on the legs. The distance

from the first sighting to the prey was 6 m. I followed a returning worker as far as I could into a tree fall tangle, 10 m from prey." The second attack involved 46 workers tackling a 6 cm long millipede within a rotten log. Once the millipede was subdued they carried it back to the nest.

Two millipedes taken from the nest by Longino were determined by R.L. Hoffmann as *Trichomorpha* sp. (Polydesmida: Chelodesmidae), and *Epinannolene* sp. (Spirostreptida: Epinannolenidae).

Comments.—This unique ant was previously only known from a restricted area in Central America. Along with *perspicax*, it represents a highly specialized form in one lineage of millipede hunters. The anterior clypeal setae are more developed than in any other of the *rastrata* group species and an interesting autapomorphy is a brief anteromedian longitudinal sulcus on the clypeus.

Specimens Examined.—COLOMBIA, Valle; COSTA RICA: Heredia: 10°20'N 84°04'W, 500m; Península de Osa, Pq. Nac. Corcovado, Sirena, < 100m, 8°28'N 83°35'W; Puntarenas: 2 km S San Vito, Finca Las Cruces, 1219 m; Río Reventazón, 4 km E Turrialba (MCZC).

Gnamptogenys bisulca Kempf and Brown

Gnamptogenys bisulca Kempf and Brown 1968: 92–3; Wheeler and Wheeler 1971:1202; Kempf 1972:112.

Diagnosis.—Longitudinal costulae on propodeal declivity, metacoxal spines hooked and triangular, not acicular; well defined transverse costulae on postpetiole sternum; propodeal spiracle as low as surrounding sculpture, not raised.

Ecology.—Occurs in mesic forested habitats. The localities suggest preference for relatively cool sites as the lowest altitudes are found at higher latitudes (10°N) and as latitude approaches the equator the localities ascend in altitude.

Comments.—Within the *strigata* complex this species is unique due to the development of its metanotal groove, and within the *striatula* group two other species also show this character state. Recent collections show a wider range than previously known.

Specimens Examined.—COLOMBIA, Chocó: 10 km SW San José del Palmar, Rio Torito, Finca Los Guaduales, 800 m, 1/4-VI-78; Valle: vic. Lago Calima, 1600 m; vic. Saladito, 1900–2100 m. COSTA RICA, Heredia: 17 km S. Puerto Viejo, 10°18'N 84°02'W, 550 m; 17 km N Volcán Barba, 10°17'N 84°05'W, 880–1020 m. ECUADOR, Pichincha: 25 km ENE Alluriquin, vía Chiribaga, 1400–1800 m; Tinalandia, 16 km SE Sto. Domingo de los Colorados, 9-VI-76; 3 km E Tandapi, 1300 m.

***Gnamptogenys boliviensis* Lattke,**
new species
(Figs. 43, 44)

Type Material.—Holotype worker. BOLIVIA, Tumupasa, W.M. Mann, leg. Deposited in the USNM. Paratypes: Seven workers deposited in the USNM; One worker and one male in each of the following: BMNH, MIZA, LACM, MCZC. One worker in MUSP. All from same locality and probably from the same nest. One specimen bears an additional label: "Mulford Biological Expedition, 1921–1922." Consultation of maps locates Tumupasa at 14°09'S 67°55'W in lowland forests of the upper Río Beni watershed.

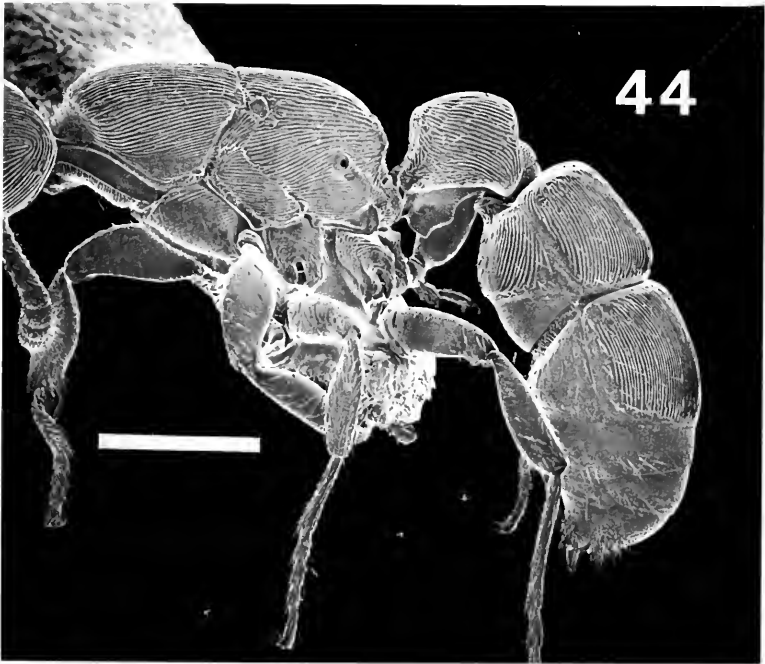
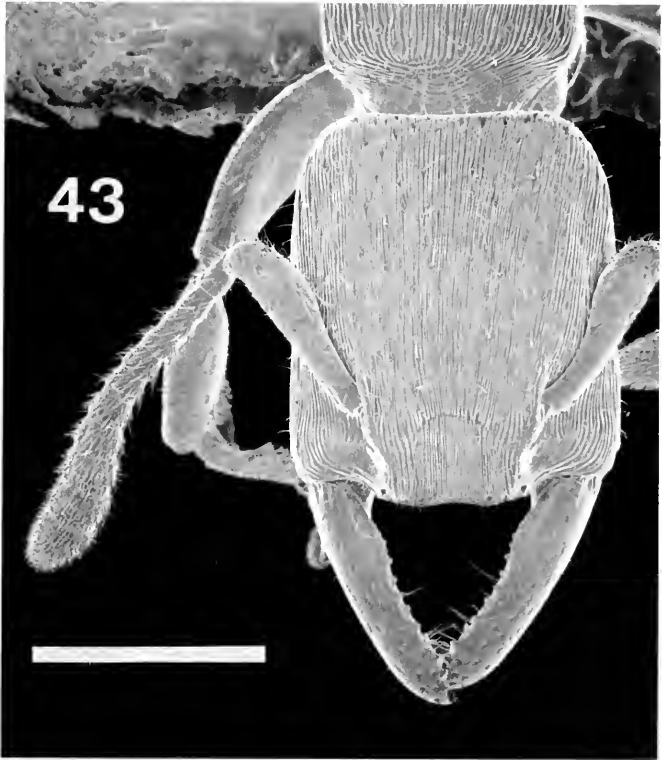
Worker.—Holotype (Paratypes) measurements: HL 0.88 (0.83–0.88); ML 0.36 (0.39–0.41); HW 0.70 (0.69–0.70); SL 0.49 (0.48–0.50); ED 0.10 (0.10–0.12); WL 1.23 (1.06–1.15) mm; CI 0.70 (0.80–0.84); SI 0.70 (0.69–0.71); OI 0.15 (0.15–0.18). $n=4$.

Head in frontal view elongate, lateral margins fairly parallel, vertexal margin concave; anterior lamella of clypeus laterally rounded and medianly convex; eyes situated at mid-length; antennae smooth and shining, dorsoventrally compressed widest apicad; mandibles smooth and

shining dorsally, with sparse punctae, subfalcate, laterobasally with small area of longitudinal rugae, including small sulcus never longer than one-fourth of the mandible; gula with longitudinal costulae, front of head with longitudinal striae.

Occasional transverse costulae on pronotal collar; mesosomal dorsum with longitudinal costulae, slightly thicker on metanotum and propodeum than on promesonotum; pronotal suture softly impressed, visible only in certain angles of view; metanotal suture deeply impressed but doesn't break longitudinal sculpture; declivitous propodeal face with oblique to transverse costulae and two superolateral ridges; pronotum laterally with transverse costulae, smooth and shining along ventral margin; anepisternum elongate and obliquely costulate; katepisternum and metepisternum with transverse costulae; costulae on metepisternum have same direction as on katepisternum, but costulae on lateral propodeal face are more horizontal; propodeal spiracle round and not prominently higher than surrounding sculpture; petiole slightly pedunculate, dorsally with longitudinal costulae, anterior face with transverse costula or rugae, sometimes partially effaced, laterally with longitudinal costulae with slight oblique tendency; node in lateral view with softly convex dorsal margin, anteriorly concave; anterior and posterior faces fairly sharply separated from dorsal face; posterior face with 4–5 convex costulae; subpetiolar process varies from subquadrate anteriorly and posteriorly concave.

Anterior postpetiolar face smooth and shining; gastric terga I and II with longitudinal striae, sternum I laterally costulate, but discal area smooth and shining as is rest of gaster; procoxa anteriorly and anterolaterally smooth and shining, posterolaterally costulate; mesocoxae with transverse costulae that tend to be effaced; dorsum of metacoxa with transverse costulae and basal, low triangular lobe; tibia and femora smooth and shining. Body fer-



Figs. 43–44. Micrographs of *G. boliviensis*. Scale bars = 0.5 mm. 43, head; 44, thorax and gaster.

ruginous brown; legs and antennae testaceous.

Queen.—Unknown.

Male.—Mandibles triangular, apical edge serrate, dorsally smooth and shining; cephalic dorsum with longitudinal striae that tend to be effaced before reaching mid-ocellus, faint transverse rugae above the posterior ocelli but rest of head smooth and shining; propodeum rugose; petiole with lateral rugulae, dorsum shining, with slight roughened aspect and median longitudinal costulae; gastric sterna and terga smooth and shining; vestigial areolea present.

Discussion.—Several specimens were found with determination labels, probably written by Mann, indicating that he recognized this species as new. *G. boliviensis* is near to *G. continua* and the possibility exists that the collection and study of more material may show them to be conspecific. In *G. continua* the sculpture is coarser, costate-costulate, and the mandibles are more robust, without a concave inner edge.

Etymology.—The name is derived from the name of the type locality country, Bolivia.

***Gnamptogenys bruchi* (Santschi)**

Ectatomma (*Parectatomma*) *bruchii* Santschi 1922: 241.

Gnamptogenys bruchi (Santschi); Brown 1958: 227; Kempf and Brown 1968:92; Kempf 1969: 275; Kempf 1972:112.

Diagnosis.—Striate body sculpture with weak transverse impressions; metacoxal process is shaped as a low, triangular lobe; clypeal lamella broadly convex anterad.

Ecology.—Apparently a predator of *Trachymyrmex* and other leaf cutting ants (Kempf and Brown, 1968:92).

Comments.—Kempf (1969) notes *bruchii* as close to *hartmanni* and that a synonymy could be possible. He also mentions the variability of the extent of impression of the metanotal groove and discards it as an indicator of species separation. This could

very well be only a variant of *hartmanni* but due to differences of sculpture on the posterior petiole face, postpetiolar sternal process and clypeal lamella, I have chosen to conserve this name until more material can be studied. The sculpture on the dorsum of the petiole can vary from longitudinal to whorled.

Specimens Examined.—ARGENTINA, Córdoba: Alta Gracia (cotype:MCZC). BRAZIL, São Paulo: Fazenda B. Rico.

***Gnamptogenys brunnea* Lattke, new species (Figs. 41,42)**

Type Material.—Holotype worker. COLOMBIA, Chocó, 10 km SW San Jose del Palmar, Finca Los Guaduales, 760 m, 2-VI-1978, C. Kugler, leg. Deposited in MIZA. Paratypes: One queen and 18 nidotype workers. Queen and 6 workers deposited in MIZA. Two workers deposited in each of the following: MCZC, LACM, BMNH, MUSP, USNM.

Worker.—Holotype (Paratypes) measurements: HL 0.90 (0.88–0.92); ML 0.30 (0.30–0.32); HW 0.74 (0.68–0.80); SL 0.74 (0.80–0.84); WL 1.20 (1.10–1.28) mm; CI 0.82 (0.77–0.87); SI 1.00 (0.95–1.09); OI 0.18 (0.16–0.18) n=5.

Cephalic dorsum longitudinally costulate; in frontal view vertexal margin concave and eyes slightly behind mid-length; mandibles triangular, with dorsal costulae, basal and apical margins with narrow smooth and shining strip that is sharply separated and lower than the rest of mandibular surface; anterior pronotal margin with 6–8 transverse costulae which arch around and become longitudinal on dorsum; mesometanotal suture well-impressed; mesonotum narrow and transverse; in lateral view dorsal propodeal face slightly depressed below rest of mesosomal dorsal margin; declivitous propodeal face distinctly separated from rest of mesosoma by low lateral ridges; mostly transverse costulae with longitudinal costulae from dorsum extending only to an-

terior one-fourth of declivitous face; petiolar node in lateral view transversely costulate and posteriorly inclined: a broad anterior convexity with sharp posterior drop and concave posterior margin; subpetiolar process shaped as an anteriorly projecting lobe; anterior postpetiolar face and sternum with transverse costulae, longitudinal on rest; costulae on the gastric tergum II finer than on preceding segment; metacoxal spine present.

Body with sparse decumbent pubescence and erect to suberect hairs; pubescence denser on legs; scapes with abundant decumbent pubescence, no erect or suberect hairs. Body reddish-brown and legs brownish-yellow.

Queen.—HL 0.98; HW 0.86; ML 0.32; SL 0.84; ED 0.18; WL 1.44 mm; CI 0.88; SI 0.97; OI 0.21. Like workers with exception of usual caste differences.

Male.—Unknown.

Discussion.—This species is close to *nigrivittata* on account of size, posteriorly tilted petiolar node, sleek appearance, subpetiolar process shape, sparse pilosity and lack of any trace of anterior petiolar peduncle. But *nigrivittata* is different in its piceous body coloration with dark brown legs, lack of metanotal groove, slightly more elevated propodeal spiracles, longer pilosity, and a sleeker petiolar node with a more prominent apical point.

Etymology.—The name comes from the Latin term for brown, *brunneus*.

Gnamptogenys concinna (Smith)

Ectatomma concinna F. Smith 1858:103.

Ectatomma (Gnamptogenys) concinnum (F. Smith); Mann 1916:406; Wheeler 1922:2.

Ectatomma (Gnamptogenys) concinnum var. *romani* Wheeler 1923:2; Brown 1958:227.

Ectatomma (Gnamptogenys) concinnum var. *conica* Borgmeier 1928:196; Brown 1958:227.

Ectatomma (Gnamptogenys) concinnum var. *semicircularis* Borgmeier 1929:195; Brown 1958:227.

Gnamptogenys concinna (Smith); Brown 1958:227; Kempf 1972:112; Lattke 1990:11.

Diagnosis.—A large finely striate species with transverse striae on propodeum, declivity medianly smooth; promesonotal suture weakly impressed or absent; mesometanotal suture deep and wide; metacoxal tooth absent, low crest or tubercle at most.

Ecology.—Consistently collected and observed on trees, this species is an arboreal nester. Longino found a nest inside a large, deep knothole and records prey items of the following: Heteroptera: Pentatomidae, Aradidae; Coleoptera: Cerambycidae, Histeridae, Platypodidae, Chrysomelidae, Tenebrionidae, and Passalidae. One observed foraging group was made up of 9 workers and a dealate queen. Observations of group foraging of up to 40 single-file workers, plus the following Longino observation, indicate trail and/or recruiting pheromone communication in this species. "The foragers walked with their gasters curled and touching the substrate. When they were together near the prey I could often make out a tiny white area (gland?) exposed at the very tip of the gaster, which other workers would investigate".

Comments.—Color can vary from ferruginous to light-brown, and the striae on the posterior nodal face may be effaced.

Specimens Examined.—BRAZIL, Amazonas: Ilha de Curari, (varzea); Amapa: Villa Amazonas. COLOMBIA, Meta: Reserva La Macarena, Caño La Curia, 580 m. COSTA RICA, Península de Osa: Pq. Nac. Corcovado, Llorona; Heredia: Finca La Selva. PANAMA, Isla Barro Colorado. PERU, Madre de Dios: 15 km E Prto. Maldonado, 200 m; Amazonas, Panguana, 9°37'S 74°56'W, 220 m; Tingo María: Valle de Monsón. TRINIDAD, Arima Valley, 152 m. VENEZUELA, Amazonas: Alto Río Mavaca, 2°02'N 65°06'W, 200m.

Gnamptogenys continua Mayr

Ectatomma (Gnamptogenys) continuum Mayr 1887:544.

Ectatomma (Gnamptogenys) exaratum Emery

1901:50; Brown 1958:303; Kempf 1972:112; Lattke 1990:13. NEW SYNONYMY.

Ectaoomma (*Gnamptogenys*) *continuum* var. *panamensis* Santschi 1931:265; Brown 1958:228, 304.

Gnamptogenys continua (Mayr); Brown 1958:228, 304; Kempf 1972:112; Lattke 1990:12.

Diagnosis.—Mandibles with linear tendency; mesometanotal suture impressed; declivitous propodeal face with small superolateral lobes; upper half with longitudinal costulae and inferior half with transverse costulae; sternal disc of postpetiole smooth; anterior nodal face rugose with some inferior transverse costulae.

Ecology.—Collected in leaf litter samples from humid forests.

Comments.—The synonymy of *exarata* was inevitable as more material accumulated and it became impossible to separate the two forms. The gap between OD and apical scape width closed. There are changes in the gauge of the costulation, degree of anterior clypeal convexity, effacement of the sculpture, shape of the subpetiolar process, extent of the petiolar peduncle, and size (HW 0.56–0.96; HL 0.64–1.16; WL 0.88–1.62). The occiput has a median dent that is most noticeable when the occiput is smooth and shining as opposed to costulate forms. Deposited in the MCZC is a specimen from Vera Cruz that was compared with the type by Brown in 1954.

Specimens Examined.—BELIZE, Caves Branch, 4 km S Belmopan. BRAZIL, Rio de Janeiro: Itatiara; São Paulo: Fazenda Conquista, Rio Preto; Guquitiba, BRE km 76. HONDURAS, La Lima. ECUADORA, Pichinchá: Tinalandia, 16 km SE Sto. Domingo del los Colorados, 680 m. COLOMBIA, Meta: Quebrada Susumuko, 23 km NW Villavicencio, 1000 m; Magdalena: Parque Tayrona, Pueblito, 360 m. MEXICO, Vera Cruz, Tuxtla, Las Hamacas, 17 km N Santiago. PERU, Panguana, 9°37'S 74°56'W, 220 m; Huanuco: 16 km SW Las Palmas, 1000 m; Pasco: Pozuzo, 1000, SURINAM, Kartabo, Bartica Dam. VENE-

ZUELA, Barinas: 17 km SSW Ciudad Bolívar, 8°02'N 70°46'W, 240 m; Guárico: 24 km N Altagracia de Orituco, 300 m.

***Gnamptogenys cuneiforma* Lattke, new species**

Type Material.—Holotype worker: PANAMA, Bocas del Toro, 8°47'N 82°11'W, 500m; 16/18-VII-87, D.M. Olson, leg. Deposited in MCZC. Paratypes: One worker deposited in MCZC and two workers deposited in MIZA, all with same locality data as the holotype.

Worker.—Holotype (Paratype) measurements: HL 0.90 (0.84–0.88); ML 0.62 (0.60–0.64); HW 0.84 (0.82–0.84); SL 0.82 (0.80–0.82); ED 0.20 (0.21–0.22); WL 1.40 (1.38–1.40) mm; CI 1.07 (1.02–1.05); SI 0.98 (0.98); OI 0.24 (0.26–0.28), $n=4$.

Head subquadrate in frontal view, sides very broadly convex, slightly wider anteriorly than posteriorly, posterior margin broadly concave, longitudinally costulate. Anterior clypeal margin with a small lamella, medianly straight and laterally rounded. A brief longitudinal carinae, thicker than surrounding sculpture, present between frontal lobes. Mandibles triangular and elongate, masticatory border concave, dorsal surface of blade convex and with longitudinal rugulae. Scapes shining and with low rugosities. Scapes without pilosity, only decumbent hairs.

Anterior pronotal face with 4–5 transverse costulae, sometimes quite rough and resembling rugae, longitudinal costulae on the dorsum posterad including the mesonotum. Metanotum and propodeum with transverse costae.

Promesonotal suture well to poorly impressed, metanotal groove well impressed. In lateral view the mesosoma has a very broadly convex dorsal margin, propodeal denticles brief and triangular, declivity concave. Sides of pronotum with regular longitudinal, slightly oblique costae. Anepisternum fulcrum shaped. Kat-episternum with a well-developed flange. Mesopleura, propodeum and dorsal two-

thirds of metapleura with transverse/oblique costae; metapleura ventrad of spiracle with longitudinal costae.

Petiole in lateral view with a low and broadly convex dorsal margin, ventral process projects anterad. Dorsally with transverse costae, posterior margin rugose. Gastric dorsum with longitudinal costulation; ventrum of postpetiole with transverse rugae along posterior half; irregular rugulae anterad to the process.

Base of foretarsus with a single stout setae opposite the strigil. Forecoxae with transverse costulae on lateral face, as well as dorsal faces of meso- and metacoxae. Legs shining and with abundant shallow punctulae. Very sparse pilosity on femora and tibiae. Color ferruginous to dark brown; mandibles, antennae and legs ferruginous.

Queen, Male.—Unknown.

Discussion.—This species may be confused with two other small *rastrata* group species: *rastrata* and *mecotyle*. It is separable from the former on account of the longer scapes (surpassing the vertexal margin), transverse costulae on the propodeum as opposed to longitudinal, and a well-defined metapleura, separated from the propodeum laterally by an impressed line, lacking in *rastrata*. The costulae of *mecotyle* have a coarse aspect in contrast with the smooth regularity in *cuneiforma*, *mecotyle* also has the striae on the scapes and dorsal mandibular surface better defined and the masticatory border lacks the concavity of *cuneiforma*.

Etymology.—The name alludes to the shape of the anepisternum.

***Gnamptogenys curvoclypeata* Lattke**

Gnamptogenys curvoclypeata Lattke 1990: 12.

Diagnosis.—Piceous species with ferruginous antenna, legs and coxae; promesonotal suture very weakly impressed, visible only with certain angles of light; meso- and metacoxae smooth and shining on median and basal lateral faces; meta-

coxae with weakly developed triangular dorsal lobe.

Ecology.—See Lattke (1990).

Comments.—See Lattke (1990).

Specimens Examined.—COLOMBIA, Amazonas: 7 km N Leticia (MCZC).

***Gnamptogenys ejuncida*, Lattke, new species (Figs. 48, 50)**

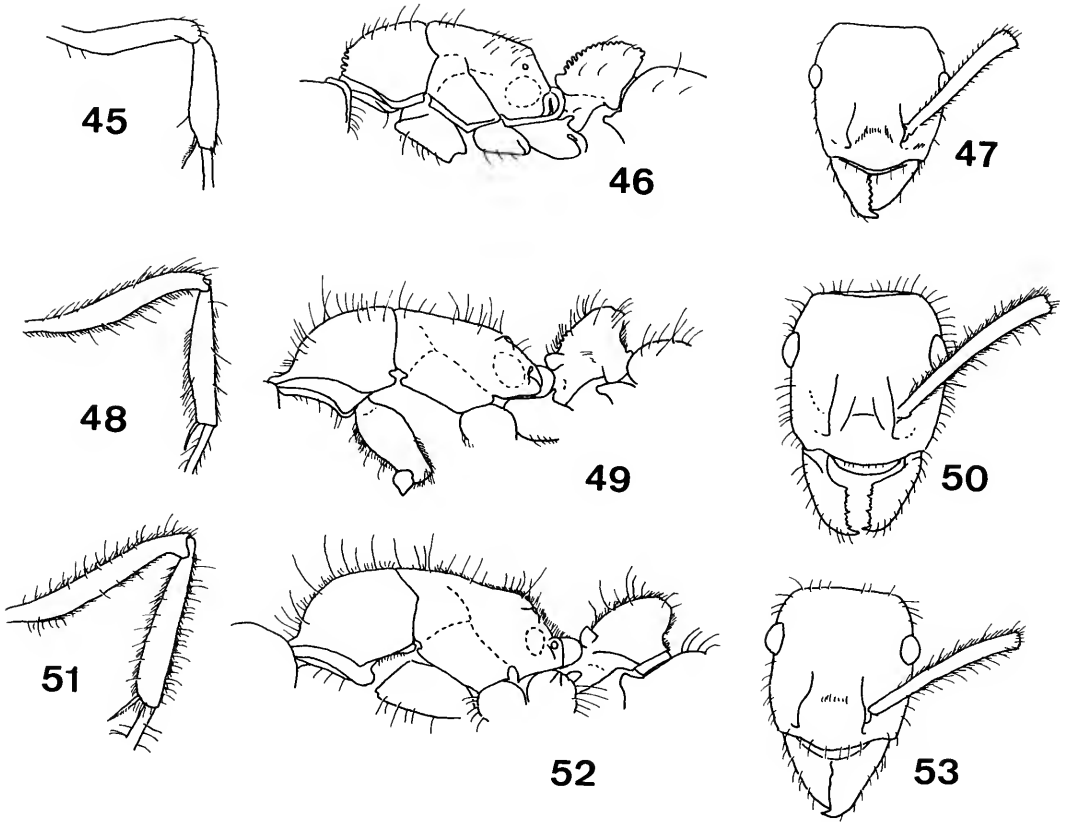
Type Material.—Holotype worker. COLOMBIA, Putumayo, Mocoa, 610 m, 4-I-77, C. Kugler, leg. Deposited in MIZA.

Worker.—Holotype measurements: HL 1.10; ML 0.26; HW 0.88; SL 1.02; ED 0.18; WL 1.54 mm, CI 0.80; SI 1.56; OI 0.21.

With head in frontal view: vertexal margins slightly convex, lateral margins broadly convex and anterior clypeal margin convex; mandibles triangular and with rugose dorsum; anterior pronotal face with six transverse costulae, dorsum with longitudinal costulae; mesonotum with anteriorly convex costulae, transverse at metanotum and posteriorly convex on dorsal propodeal face; anepisternum with three transverse costulae that descend from mesonotum; rest of mesosomal side obliquely costulate, some curve around propodeal spiracles; declivitous propodeal face with longitudinal costulae; in lateral view dorsal mesosomal outline evenly convex, with no abrupt breaks or depressions; petiolar node posteriorly inclined; in lateral view transversely costulate with convex anterior margin, concave posterior margin and overhanging apex; subpetiolar process triangular and projecting anterad. Anterior face to dorsal two-thirds of postpetiolar dorsum with transverse costulae; rest of gastric sculpture longitudinal; postpetiolar sternum anteriorly transversely costulate, posteriorly divergent; transverse costulae on procoxae and anterior faces of meso- and metacoxae; metacoxal tooth well developed. Abundant suberect hairs and pubescence on body and extremities.

Queen, Male.—Unknown.

Ecology.—Unknown.



Figs. 45–53. Lateral view of posterior leg, mesosoma and petiole, and frontal view of head. 45–47, *G. extra*; 48–50, *G. ejuncida*; 51–53, *G. pilosa*.

Discussion.—On account of size, sculpture, pilosity and posteriorly inclined petiole node this species seems to be most closely related to *pilosa*, a very similar species found in an Andean canyon NW of Cali, Colombia. The sculpture of *pilosa* is much finer and its pilosity is a bit denser, including abundant erect hairs, practically lacking in *ejuncida*. The presence of erect to suberect hairs in *pilosa* vs. subdecumbent to decumbent hairs in *ejuncida* is especially notable on the femora. In lateral view the angle formed by the junction of the dorsal and declivitous propodeal faces is greater in *ejuncida* than in *pilosa*, giving it a more slender appearance.

Etymology.—This sleek species inspired the use of the Latin word for slender, *ejuncida*.

***Gnamptogenys ericae* Forel, revalidated**

Gnamptogenys tornata var. *ericae* Forel 1912:33; Brown 1958:229.

Gnamptogenys sulcata (F. Smith); Brown 1958:329; Lattke 1989:24.

Gnamptogenys sulcatum bufonum Weber 1938:208. NEW SYNONYMY.

Diagnosis.—Mandibles subtriangular; posterior mesosomal dorsum and propodeum with longitudinal costulae, transverse sutures barely visible under certain angles of lighting; small metacoxal tooth. Body black; antennae, legs and mandibles brown to dark brown.

Ecology.—Can be found nesting in disturbed forests and coffee plantations as well as in undisturbed forests.

Comments.—Much confusion has accu-

mulated regarding the identity of this species and the similar *sulcata*. Many previous references to *sulcata* are actually *ericae*, but the confusion makes it quite difficult to distinguish between each reference. Dr. Ivan Löbl of the MHNG kindly examined the *ericae* type and confirmed the longitudinal direction of the costulae on the posterior face of the node of the specimen. A specimen in the MCZC from Guiana with a determination label as *bufonum* in N. Weber's handwriting and another label stating "in *Bufo marinus* stomach" coincides with the information in Weber's description. Even though it has no label designating it as a type, it seems reasonable to conclude that Weber's *bufonum* is a synonym of *ericae*. For a broader discussion on the separation of the forms known as *tornata* and *sulcata* the reader should turn to the "Discussion" for *G. sulcata*. Color in this species is relatively constant but occasional ferruginous, brown or mottled specimens will turn up. Size and shape of the petiolar node does not vary as much as in *sulcata*. Workers seem to always have longitudinal costulae on the propodeal declivity, though queens may have transverse costulae.

Specimens Examined.—BOLIVIA, Rosario. COLOMBIA, Magdalena: Minca, 610 m; Guajira: Serranía de Macuira, 7 km S Nazareth, 70–200m; Meta: San Juan de Arama, 914m; La Macarena, Río Guayabero, 260m; 65 km E Puerto López. GUIANA, Forest Settlement, R. Mazaruni. TRINIDAD, Port of Spain, Federation Park. VENEZUELA, Mérida: Santa Cruz de Mora, 600m; Guárico: Hato Masaguaral; Bolívar: Campamento Río Grande, 8°07'N 61°48'W, 280 m; Anzoátegui: 20 km S El Tigre.

***Gnamptogenys extra* Lattke, new species**
(Figs. 45–47)

Type Material.—Holotype worker. EC-UADOR, Pichincha: Tinalandia, 16 km SE Santo Domingo de Los Colorados, VI-1976, S. & J. Peck, leg. Deposited in MIZA.

Paratypes: (1) One worker with the same data as the holotype. Deposited in MCZC. (2) Two workers from COLOMBIA, Chocó: Lloró, Vereda Peñaloza, 26-III-1988, V. Jaimes, leg. One worker in BMNH and LACM, respectively.

Worker.—Holotype (Paratypes) measurements: HL 1.20 (1.10–1.12); HW 1.00 (0.94–1.00); ML 0.34 (0.30–0.34); ED 0.16 (0.14–0.18); SL 1.26 (1.00–1.20); WL 1.68 (1.44–1.50) mm; CI 0.83 (0.85–0.98); SI 1.26 (1.06–1.20); IO 0.16 (0.15–0.19) $n=4$.

With head in frontal view: vertexal margin straight, laterally convex with eyes slightly behind midlength, and anterior clypeal margin convex; mandibles triangular with dorsal striae; scapes relatively thick in appearance and surpassing vertexal margin; vertex with 2–3 transverse costulae; anterior pronotal face with 5–7 transverse costulae, dorsally with anteriorly arching costulae; costulae on mesonotal concentric or longitudinal; costulae on metanotum and dorsal propodeal face transverse to longitudinal, sometimes arched; declivitous propodeal face with longitudinal costulae that diverge posteriorly, basally with 2–3 transverse costulae.

Petiolar node in lateral view subquadrate, with broad anterodorsal convexity and sharp posterior drop with overhanging apex; subpetiolar apex is an anteriorly projecting lobe; anterior postpetiolar face with transverse costulae that arch back and become longitudinal posteriorly; rest of dorsal gastric costulae longitudinal, divergent on posterior postpetiolar sternum; ventral stridulitrum present on fourth abdominal segment. Scapes with abundant decumbent pilosity and no suberect or subdecumbent hairs; decumbent pilosity also present on coxae and legs, with no standing hairs; sparse suberect hairs on rest of body. Body dark brown, legs and antennae slightly lighter.

Male, Female.—Unknown.

Discussion.—This species has a fairly pointed petiolar node apex, but it doesn't

approach the extremely pointed condition of *G. acuta*. The node is more robust and subquadrate (lateral view) than in other *porcata* subgroup species and is reminiscent of the condition in *G. tortuolosa*. This species could be closely related to *G. striatula* on account of the node shape (erect) and the lacking anterior peduncle.

***Gnamptogenys fernandezi* Lattke**

Gnamptogenys fernandezi Lattke 1990: 14.

Diagnosis.—Triangular mandibles with a smooth and shining dorsum; anterior lamella of clypeus convex; promesonotal suture lightly impressed and mesometanotal suture absent; low, elongate petiole, posterodorsally bluntly pointed; metacoxal teeth absent.

Ecology.—A rarely collected, but fairly widespread species in n South America. In Venezuela known only from 2 forested localities in the Cordillera de la Costa between 650–1100 m.

Comments.—See Lattke (1990).

Specimens Examined.—COLOMBIA: Valle: 50 m (no other data). ECUADOR. Morora: Santiago, Los Tayos. PERU, Madre de Dios: 5 km SE Prto. Maldonado, Río Tambopata, 260m; Cuzco Amazónico, 15 km NE Prto. Maldonado, 200m. VENEZUELA, Carabobo: Hacienda Palmichal, Canoabo 900 m.

***Gnamptogenys gentryi* Lattke, new species**

Type Material.—Holotype worker. COLOMBIA, Valle, 2250 m, Insp. Pance, Reserva Natural Hato Viejo, J.B. Hillaire, leg. Deposited in MIZA. Thank you to Fernando Fernández for making the specimen available.

Worker.—Holotype measurements: HL 1.22; ML 0.32; HW 0.92; ED 0.22; SL 1.04; WL 1.64 mm; CI 0.75; SI 1.13; OI 0.24.

Head in frontal view elongate, anterior clypeal margin convex, posterior margin concave, eyes relatively flat, finely costulate throughout, though diverging at ver-

tex, with a band of three transverse costulae next to the vertexal carinae; mandibles triangular, frontal surface rugulose. Scapes mostly smooth and shining except for sparse punctulae.

Pronotal dorsum with whorled costulae almost enclosing 3 brief longitudinal costulae, rest of mesosomal dorsum with longitudinal costulae, metanotal groove deeper than pronotal suture. In lateral view the mesosoma has a convex pronotal profile that becomes an inclined and more or less straight slope that bends sharply at the propodeal declivity, which has a broadly concave profile. Node in lateral view tilted backwards, with oblique to longitudinal rugulae laterally and transverse costulae on the anterior and posterior faces, ventral process subquadrate, with anterior corner projecting more than posterior corner. Gastric tergite I mostly smooth and shining except for anterior face which has a small area of transverse costulae and the sternite with transverse striae; the rest of the gaster is smooth and shining. Color black.

Queen, Male.—Unknown.

Discussion.—This *striatula* group species is quite easy to separate from all others just considering the presence of a metanotal groove and the mostly smooth and shining gaster.

Etymology.—Named in honor of the late botanist Alwyn Gentry, he died in the line of duty in the Andes of Ecuador.

***Gnamptogenys gracilis* Santschi**

Holcoponera gracilis Santschi 1929:468.

Gnamptogenys gracilis (Santschi); Brown 1958: 228, 232; Kempf 1972:112; Lattke 1990:17.

Diagnosis.—Finely costulae; pronotal costulae concentric to arched; mesonotum frequently with longitudinal costulae surrounded by concentric costulae; metanotum and propodeal dorsum with transverse costulae, and longitudinal on declivitous propodeal face; subpetiolar process anteriorly triangular and posteriorly angular.

Ecology.—This is an epigaeic forager known only from primary and secondary wet forests of the Guiana Shield and its remnants in the Venezuelan Amazonas, mostly between altitudes of 850–1600 m. Within the range of 1000–1200 it can be locally abundant. One record from 550 is next to Angel Falls. This suggests that proximity with the higher forested talus slopes of Auyán Tepuy could explain its occurrence at such a low elevation. This species obviously prefers cool, mesic habitats. This distribution plus climatic evidence (Schubert 1988) suggests that *G. gracilis* may have been more widely distributed in this area during the last glacial period.

Comments.—On account of size, similar sculpture, posteriorly inclined node and fair amount of pilosity, its nearest relative appears to be *pilosa*, also an apparent endemic, of the Colombian Cordillera N and NNW of Cali. An occasional specimen may have a second, smaller seta just below the prominent seta of the foretarsal base.

Specimens Examined.—VENEZUELA, Bolívar: Auyán Tepuy, Sector Aonda, 6°02'N 62°37'W, 1600 m; Auyán Tepui, Cañón del Diablo, Isla Ratón, 550 m; San Ignacio de Yuruaní, 5°00'N 61°08'W, 800 m (MIZA).

Gnamptogenys haenschi Emery

Gnamptogenys haenschi Emery 1902:27; Brown 1958:302; Kempf 1972:112.

Diagnosis.—Vertexal margin concave in frontal view; mandibles with longitudinal costulae; declivitous propodeal face with longitudinal striae superiorly and basally transverse rugae; petiolar node transverse; postpetiolar sternum mostly transversely strigulate; no metacoxal tooth.

Ecology.—This species inhabits forest and apparently nests in rotten wood as well as in soil. It has also been taken in oil palm plantations. Some specimens were collected from carrion traps baited with

iguana meat. Longino (pers. comm.) reports finding a nest beneath a rotten log; the ants burrowed into the soil on exposure.

Comments.—This species is possibly the only survivor of an otherwise extinct lineage in the genus. See discussion on phylogeny of the different species groups.

Specimens.—BOLIVIA, Lower Río Madidi; El Montero, 70 km N Sta. Cruz. COLOMBIA, Cauca: Isla La Gorgona; Guajira: Quebrada Guacoche, vic. Don Diego, 10 m; Magdalena: 4 km N San Pablo, 10°57'N 74°03'W, 550 m. COSTA RICA, Península de Osa: Corcovado, 8°28'N 83°35'W; Heredia: La Selva; 3 km S Prto. Viejo, 10°26'N 84°00'W, 50m. ECUADOR, Napo: Prto. Misahualli, 350 m. PERU, Tingo María: Valle de Monsón; Puerto Maldonado, 260m; Loreto: Ramón Castillo, 5 km NW Leticia. PANAMA, Darién: Río Tacaruna, 580m. VENEZUELA, Alto Río Siapa, 1°40'N 64°35'W, 530m.

Gnamptogenys hartmani (Wheeler)

Ectatomma (*Parectatomma*) *hartmani* Wheeler 1915:390.

Gnamptogenys hartmani (Wheeler); Brown 1958: 228, 302; Echols, 1964:137; Kempf 1972:112; MacKay 1988:127.

Gnamptogenys nigrifrons Borgmeier 1948; Brown 1958: 228, 236; Kempf 1972:114. NEW SYNONYMY.

Gnamptogenys turmalis Kempf and Brown 1968: 93; Kempf 1972:116. NEW SYNONYMY.

Diagnosis.—Superolateral corners of declivitous propodeal face with small lobes or carinae; mandibles triangular to subtriangular; metanotal groove vaguely impressed and posterior nodal face has longitudinal costulae; metacoxal dorsum with lobes; subpetiolar process subquadrate.

Ecology.—One record from soil in a banana farm and another from soil in a destroyed *Trachymyrmex* nest. These ants have on several occasions been reported as predators of *Trachymyrmex* ants (Echols, 1964:137; Kempf and Brown, 1968:94). J.

Longino (pers. comm.) reports from Costa Rican field notes of Dana Myer: "a nest was found found in leaf litter amidst the remains of a *Trachymrmex* nest and many cut up workers and a queen of the attines were also found along with many wounded *Gnamptogenys* workers." Longino has observed this species carrying its brood in a loose 3 m column, fleeing from raiding *Eciton*. One specimen was taken from the stomach contents of *Dendrobates lecomelas*.

Comments.—Kempf and Brown described *G. turmalis* as being close to *G. nigrifrons* but slightly larger and more robust, with finer sculpturing and a uniform ferruginous color. These authors realized that *G. hartmani*, *G. nigrifrons* and *G. turmalis* were so close as to constitute possible synonyms, and they were right. The study of specimens at hand show colors vary enough to make it an unreliable character for separating species and the same is true for irregularities in the sculpture. Specimens from more southern localities have finer costulation. Also found to vary continuously was the length vs. width of the petiolar node, as well as other size indicators.

Specimens Examined.—BRAZIL, Bahia, Ilheus-Itab., km 22, (CEPEC). COSTA RICA, Península de Osa: Sirena, 8°28'N 83°35'W, 50m. GUYANA, Kartabo; HONDURAS, La Lima, Zapote farm. MEXICO, Tamaulipas: 10 km W EL Encino, 23°N 08'W 99°10'W; PANAMA, Isla Barro Colorado. PERU, Valle de Chanchamayo, 800 m. USA, Louisiana: Lucky; Texas: Benton-Rio Grande State Park, 30. VENEZUELA, Amazonas, vic. Cerro Ya-Pakana.

***Gnamptogenys haytiana* (Wheeler and Mann)**

Spaniopone haytiana Wheeler and Mann 1911:11.
Gnamptogenys haytiana (Wheeler and Mann);
Brown 1958:228, 316; Kempf 1972:113.

Diagnosis.—Petiole node disciform, with anterior and posterior faces more or less parallel to one another, dorsal and lateral

nodal faces with transverse rugulae; metanotal groove barely impressed; propodeal spiracles mounted on turrets at mid-height of the lateral edge of declivitous propodeal face.

Ecology.—Taken from forest and coffee plantation leaf litter. The dramatic deforestation of Hispaniola has considerably reduced the range of this species.

Comments.—Endemic to Hispaniola Island. On account of the yellowish color, more pronounced curvature of the second gastric segment and different sculpture, this species is outstanding amongst the other members of its species complex. It is possible that it represents an independent development from the *strigata* complex. The holotype was examined in the MCZC.

Specimens Examined.—DOMINICAN REPUBLIC, Barahana: 2 km N Polo, 1000m.

***Gnamptogenys horni* Santschi**

Gnamptogenys regularis horni Santschi 1929:475.
Gnamptogenys horni Santschi; Brown 1958:228, 235, 316; Kempf 1961:491; Kempf 1972:113; Lattke 1990:17.

Diagnosis.—Subtriangular mandibles; dorsum of petiolar node with posteromedian longitudinal costulae, transversely arched anteriorly; episternal costulae curve on to declivitous propodeal face. Body dark brown; legs and antennae ferruginous.

Ecology.—A series was taken from the stomach of *Colostethus nubicola*. See Lattke 1990.

Comments.—This common species has a wide range in the neotropics. There is fair size variation and smaller specimens usually have more vermiculate costulation. The position of the propodeal spiracle can vary from mid-height to below mid-height and the metacoxal tooth from triangular to denticulate. Nests of small forms can sometimes be found in the same locality as larger forms. Intermediates were found in other localities. A specimen labelled as a "cotype" was examined in the MCZC.

Specimens Examined.—BRAZIL, Amazonas: Rio Taruma; Benjamin Constant; Reserva Ducke; via Manaus–Itacoatiara km 50; Manaus; Rondonia: Vilhema; Pará: Carajás; Utinga Tract vic. Belém. BOLIVIA, Caranavi, vic. radio, 800m. COLOMBIA, Chocó, Río Napipi. ECUADOR, Pichincha: Estación Río Palenque; Sucua; Morona: Santiago, Los Tayos; Esmeraldas: 48 km S Atacames. GUYANA, Kamakusa. PANAMA, Isla Barro Colorado. PERU, Panguana, 9°37'S 74°56'W, 220m; Tingo María: Valle del Monsón. SURINAM, Tambahredjo; Dirkshoop; La Poolle; Maripahueuei, Vank. VENEZUELA, Amazonas: Alto Río Mavaca, 2°02'N 65°06'W, 200m; Alto Río Siapa, 1°40'N 64°35'W, 600m.

***Gnamptogenys ilimani* Lattke,
new species**

Type Material.—Holotype worker. BOLIVIA, 22 km N Caranavi, Vivero Ilimani, 1700 m, 22-VI-81, C. Kugler, leg. Primary forest clearing with *Cinchona*, nest in rotten wood. Deposited in the MIZA. Paratypes: paranidotypic workers from the same nest as the holotype. Deposited in each of the following: BMNH, LACM, MUSP, MCZC, MIZA.

Worker.—Holotypes (Paratypes) measurements: HL 0.90 (0.84–0.90); HW 0.78 (0.72–0.78); ML 0.30 (0.26–0.32); ED 0.14 (0.14–0.18); SL 0.70 (0.70–0.72); WL 1.20 (1.12–1.20) mm; CI 0.87 (0.84–0.88); SI 0.90 (0.92–0.97); OI 0.19 (0.18–0.27) $n=5$.

Coarsely costulate *strigata* group species. With head in frontal view vertexal margin convex; anterior pronotal face with 3–4 costulae that sharply bend back laterally to become longitudinal; declivitous propodeal face with longitudinal costulae; node anteroposteriorly compressed, its posterior face sharply marginate laterally with a flat to slightly concave surface and effaced sculpture; anterior postpetiolar face with 2–3 transverse costulae, rest longitudinal; postpetiolar sternum with longitudinal costulae; lateral mesocoxal face with oblique, rough costulae and that

of metacoxae with rough rugulae; metacoxal tooth low and triangular. Body black with yellow-brown legs and scapes; abundant appressed pilosity on legs and scapes, but no standing hairs.

Queen.—Measurements: HL 0.88 (0.88); HW 0.72 (0.74); ED 0.20 (0.18); SL 0.72 (0.72); WL 1.28 (1.20) $n=2$. Differences from workers are the usual; caste differences, though the node is more disciform.

Male.—Unknown.

Discussion.—This species is nearest to *G. strigata* and *G. pittieri* but they are separable on several on several accounts: the posterior petiolar node face is not sharply set off and has raised costulae; in dorsal view their node is anteriorly convex, not straight; standing hairs on the body and especially the scapes are abundant, scape pilosity is longer. In *G. pittieri* the anterior transverse costulae of the pronotum curve around gently at the sides.

Etymology.—The species name alludes to the type locality.

***Gnamptogenys ingeborgae* Brown**

Gnamptogenys ingeborgae Brown 1992:279.

Diagnosis.—Mandibular masticatory margin denticulate, promesonotal suture present, at least partially, and the longitudinal costulae on the propodeal dorsum and postpetiolar tergite is frequently ill-defined to effaced.

Ecology.—A specialized millipede feeder from Colombia. See Brown 1992.

Comments.—See Brown 1992.

Specimens Examined.—COLOMBIA, Cundinamarca, Bogotá–Villavicencio road, km 79, 1100 m (type series: MCZC).

***Gnamptogenys interrupta* Mayr**

Ectatomma (*Gnamptogenys*) *interruptum* Mayr 1887:543.

Gnamptogenys interruptum (Mayr); Mann 1922:3; Brown 1958:228, 303; Kempf 1968:377; Kempf 1972: 113; Lattke 1990:18.

Diagnosis.—Sublinear mandibles. Cephalic dorsum, mesosoma, and gastric ter-

gum I with longitudinal costulae; gastric tergum II smooth; pleura also with smooth patches; metacoxal tooth absent. Body reddish brown; legs and antennae ferruginous.

Ecology.—Found in humid forests of lowlands and mountains (cloud forest). Taken from leaf litter samples and beneath bark of rotting logs on ground.

Comments.—Lateral mesosomal costulae can be effaced to a variable degree and the second gastric segment can occasionally have weak longitudinal costulae, medianly effaced. Declivitous propodeal face with longitudinal costulae and weakly developed anterolateral lobes.

Specimens Examined.—COLOMBIA, Magdalena: 3 km SE Minca, 11°08'N 74°06'W, 1050m; Valle: Puerto Merizalde, 10 m. COSTA RICA, Puntarenas: Monteverde, 10°18'N 84°48'W, 1500m. HONDURAS, Lombardia; JAMAICA, Mandeville.

***Gnamptogenys kempfi* Lenko**

Gnamptogenys kempfi Lenko 1964:257; Kempf 1972:114.

Diagnosis.—Mandibles subtriangular, dorsally smooth and shining. transverse costulae on mesosomal dorsum and node, no apparent transverse sutures on mesosomal dorsum. Propodeal spiracle large and metacoxal tooth present.

Ecology.—Apparently from lowland forest, one nest was found in rotten wood on the ground.

Comments.—A widespread but uncommon species.

Specimens Examined.—COLOMBIA, Amazonas: 7 km N Leticia. PERU, Pan-guana, 9°37'S 74°56'W, 220m (MCZC).

***Gnamptogenys lanei* Kempf**

Gnamptogenys lanei Kempf 1960:388–90; Kempf 1968:377; Kempf 1970: 325; Kempf 1972:114.

Diagnosis.—Relatively small eyes; clypeal lamella medianly concave; promesonotal suture vestigial and small denticles on

the propodeum; node elongate, with transverse costulae.

Ecology.—Its morphology puts it in the *rastrata* group of millipede hunters.

Comments.—Kempf 1968:377 reports a series with transverse costulae on the anterior pronotal face, differing from the longitudinal sculpture of the type series.

Material.—BRAZIL, Pará: Belem, Rio Guama (MUSP).

***Gnamptogenys laticephala* Lattke, new species (Figs. 54, 55)**

Type Material.—Holotype worker. EC-UADOR, Guayas: 3 km S Bucay, 24-VII-73, W.L. Brown, leg. Deposited in MCZC.

Worker.—Holotype measurements: HL 1.71; ML 1.01; HW 1.94; SL 1.53; ED 0.34; WL 2.32 mm; CI 1.13; SI 0.79; OI 0.18.

Head in frontal view broad, vertexal margin fairly straight, lateral margins slightly convex and anteriorly diverging; eyes large and situated at cephalic mid-length; anterior clypeal lamella broadly concave with lateral triangular teeth near mandibular insertions; clypeus with two small anteriorly projecting lobes between anterior border of antennal fossae and anterior lamella; cephalic dorsum with longitudinal rugae that diverge slightly posterad on to vertex; rugae between frontal lobes and eyes more irregular than rugae between and behind frontal lobes; abundant piligerous punctures present. Antennal scapes smooth and shining, surpassing vertexal margin; gula with median longitudinal carinae and transverse costae at each side; mandibles falcate, longitudinally costulate with interior glabrous sulcus that ends at apical tooth, basal tooth marks the end of basal margin and is followed by two more pre-apical teeth; anterior pronotal face opaque, not as shiny as rest of pronotum and with faint transverse rugulae; mesosomal dorsum with parallel longitudinal costulae, promesonotal suture well impressed but does not break longitudinal sculpture, mesometa-

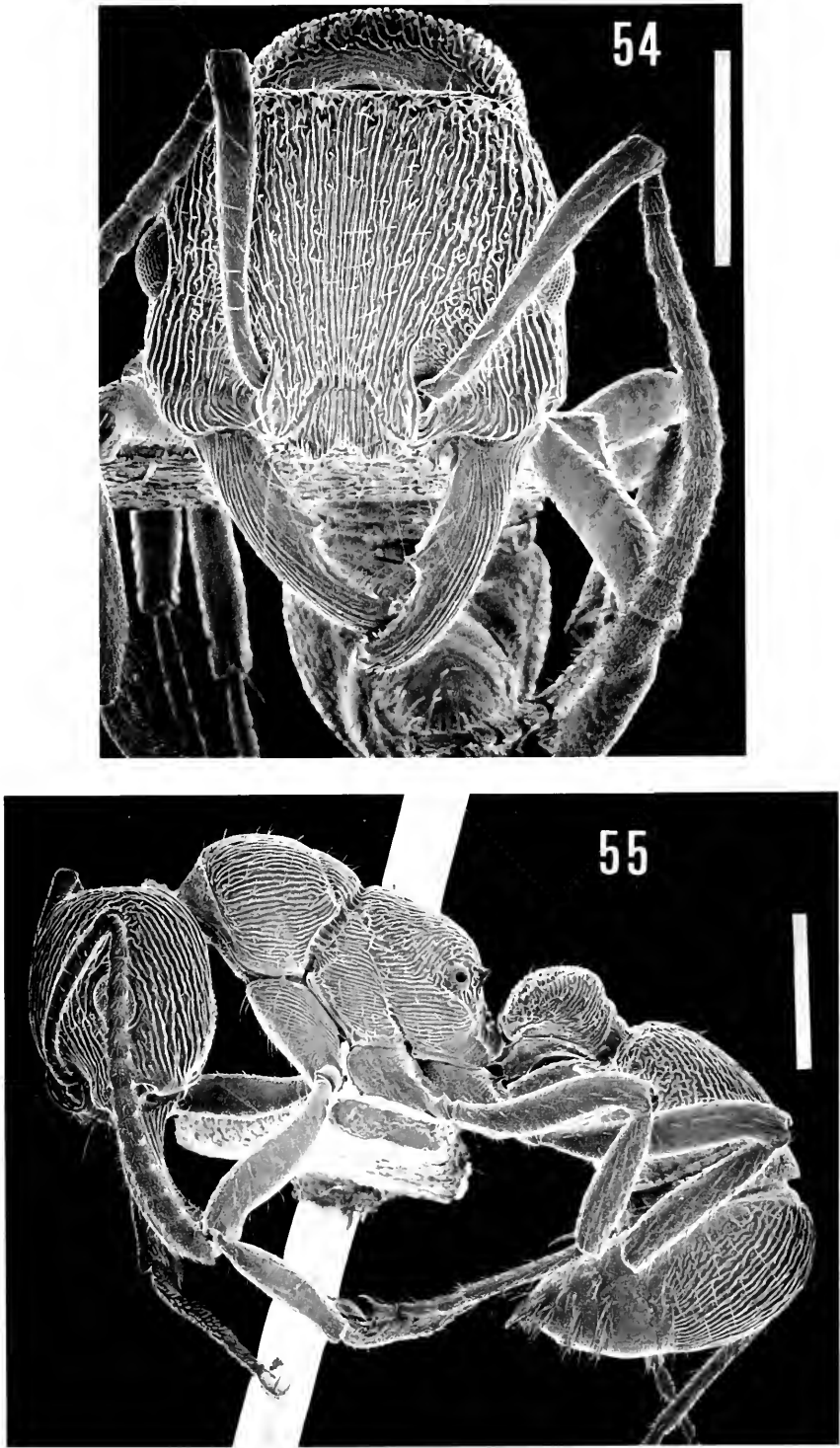


Fig. 54-55. Micrographs of *G. laticephala*. Scale bars = 1.0 mm. 54, head; 55, body.

notal suture deep and interrupting sculpture except for some ridges that join a few costulae on either side of suture; lateral pronotal face with slightly oblique parallel costulae; pronotal-mesopleural suture very broad and deep; meso- and metepisterna with parallel, longitudinal costulae; mesometepisternal suture well impressed and metepisternal-propodeal suture distinct; metepisternal lobe well developed; declivitous propodeal face with longitudinal costulae; petiolar node in lateral view low, anterodorsal margin convex and posterodorsal margin sharply convex; transversely costulate; subpetiolar process anteriorly triangular, with slightly rounded posterior lobe.

Postpetiolar costulation longitudinal, weakly roughened and becoming rugulose laterally, ventrally with transverse costulae that tend to fade medially; gastric tergum II strongly vaulted anteroventrally with dorsal and lateral sculpture as on preceding segment; apical gastric segments with faint transverse strigulae, tending to smooth and shining; anterior face of procoxae smooth and shining laterally with oblique costulae; meso- and metacoxae laterally smooth and shining, dorsally transversely costulate; metacoxal teeth well developed; body with sparse suberect and decumbent hairs, longest on gastric apex and clypeus, no appressed pilosity on scapes, just suberect and decumbent hairs. Mesosoma dark reddish brown; head, node and gaster darker; legs and antennae brown; mandibles brown to yellow brown.

Queen, Male.—Unknown.

Discussion.—The two lobes between the antennal fossae and clypeal lamella distinguish this species from all other New World members of the group, which lack such lobes, including its closest relative, *banksi*. Other characters in which *banksi* differs are the following: areolate sculpture on the cephalic dorsum, occiput and anterior pronotal face with transverse rugae, deep lateral and mesonotal pits for

the spiracles (such pits lacking in *fraudatrix*), pronotal suture interrupts sculpture, and the inner mandibular mandibular sulcus only reaches the basal angle. In general the sculpture of *banksi* is rougher, mostly of gaster I, which is reticulate rugose and gaster II has rough, widely spaced, dorsal longitudinal rugae, becoming more irregular laterally. The form of the pronotal-mesopleural suture and the lobes formed by the pronotum and anepisternum at the base of the suture are reminiscent of some *minuta* group species. The possibility exists that this could be an aberrant specimen of *banksi* (it was found determined as such), but given the observed differences I have opted for the most conservative course. It is hoped that the capture of additional specimens may throw more light onto the status of *laticephala*.

Etymology.—The name alludes to the relatively broad head when seen in frontal view.

***Gnamptogenys lineolata* Brown**

Gnamptogenys lineolata Brown 1992:275.

Diagnosis.—Head in frontal view subquadrate, scapes smooth and shining; mandibles denticulate; sculpturing of body striate, lacking propodeal denticle.

Ecology.—A specialized millipede feeder endemic to Hispaniola.

Comments.—See Brown 1992.

Specimens Examined.—DOMINICAN REPUBLIC, La Vega, La Cienaga, 1100 m.

***Gnamptogenys lucaris* Kempf**

Ectatomma tornatum Luederwalt 1926:236 (nec Roger 1862).

Gnamptogenys lucaris Kempf 1968:379; Kempf 1972:114.

Diagnosis.—Mandibles subtriangular; clypeal lamella laterally bluntly rectangular, not acutely dentate; propodeum with longitudinal costulae; node low, its declivitous face narrow.

Ecology.—Luederwalt (1926) reports a

specimen on a shrub devouring the remains of a beetle.

Comments.—This species is very close to *G. siapensis* and the possibility exists that they are conspecific.

Specimens Examined.—None.

Gnamptogenys mecotyle Brown

Gnamptogenys mecotyle Brown 1958:318; Kempf 1972:114.

Diagnosis.—Promesonotal suture and metanotal groove impressed but not breaking sculpture; propodeal spiracle opening large and round, right behind teeth; metacoxal teeth long and sharp; occipital carinae wide and visible in frontal view; anterior clypeal lamella laterally rounded and anteriorly straight to very broadly convex.

Ecology.—Millipede feeder captured in litter samples from wet forest. Some specimens found in stomach contents of *Dendrobates histrionicus*.

Comments.—The cephalic sculpture can vary from evenly costulate to roughly rugose and the petiole length vs. width is also variable.

Specimens Examined.—COLOMBIA, Antioquia, Providencia, Estación Biológica; Chocó: Serranía de Baudó, Camino de Yupe, 500–700m; Amazonas: 7 km N Leticia. COSTA RICA, Puntarenas: 6 km SW Monteverde. 10°16'N 84°50'W, 900m. PANAMA, Isla Barro Colorado.

Gnamptogenys mediatrix Brown

Gnamptogenys mediatrix Brown 1958:362; Kempf 1972:114.

Diagnosis.—Mandibles elongate and triangular, their basal $\frac{2}{3}$ rugulose and apical $\frac{1}{3}$ smooth and shining; clypeal lamella medianly concave; scapes with no erect hairs; petiolar costulation mostly transverse, node broader than long; metacoxal teeth very slender, propodeal teeth short.

Ecology.—Apparently of lowland forests, one series taken from a varzea habitat. Its morphology puts it within the *ras-*

trata group, and it is quite probably a millipede hunter.

Comments.—Rarely collected, it is a close relative of *G. laticephala*.

Specimens Examined.—BRAZIL, Amazonas: Ilha de Curarí; Pará; Igarapé Maná (MCZC).

Gnamptogenys menozii (Borgmeier)

Ectatomma (*Parectatomma*) *menozzi* Borgmeier 1928:32

Gnamptogenys menozzi (Borgmeier); Brown 1958: 228, 316, 321; Kempf 1972:113

Ectatomma (*Parectatomma*) *schubarti* Borgmeier 1948:198. NEW SYNONYMY.

Gnamptogenys schubarti (Borgmeier); Brown 1958:316; Kempf 1960a:390; Kempf 1972:114.

Diagnosis.—Eyes convex; mandibles; promesonotal suture impressed but not deep, metanotal groove very deep; propodeal teeth short; mesosoma longitudinally costulate.

Ecology.—Found in forested areas, including montane forests.

Comments.—Borgmeier described *G. schubarti* upon characters always “a bit more” than for *G. menozzi* and it is curious to note how authors frequently refer to these two forms together when discussing their differences from other species. Brown (1958:316) discusses differences between the two forms: size, number of costulae, color and the shape of the subpetiolar process. He also admits that the forms could belong to one species. Size differences between the two forms overlap and the color and gauge of the costulation are also continuously variable. The differences in the shape of the subpetiolar process are well within infraspecific variation, at least as observed in other *Gnamptogenys*.

Specimens Examined.—BRAZIL, Rio Grande do Sul (*menozzi* cotype: MUSP); Sao Paulo: Monte Alegre, 900m (*schubarti* cotype: MUSP); Rio Corocovado; Espirito Santo: Res. Nova Lombardia, 4 km N Santa Tereza, 900 m.

Gnamptogenys mina (Brown)

Holcoponera mina Brown 1957:494.

Gnamptogenys mina Brown 1958:220, 228; Kempf 1972:114; Lattke 1990:18.

Diagnosis.—Mandibular dorsum smooth and shining and apex of scapes surpassing the vertexal margin; declivitous propodeal face flat and separated from the dorsal face by a sharp angle; propodeal spiracles elevated at the apex of cylindrical tubercles.

Ecology.—Found in leaf litter and earth samples from humid forests.

Comments.—The series from near Kavanayen show very sharply defined costulae with fine vermiculation in contrast with the glazed and effaced aspect of other series.

Specimens Examined.—COLOMBIA, Putumayo: Villa Garzón (MCZC). VENEZUELA, Bolívar: 10 km E Kavanayen, 1200 m (MIZA).

Gnamptogenys moelleri (Forel)

Holcoponera moelleri Forel 1912:34; Mann 1916: 404.

Holcoponera teffensis Santschi 1929:449. NEW SYNONYMY.

Holcoponera teffensis var. *concinna* Santschi 1929: 449 (nec. F. Smith 1858); Brown 1958:229.

Holcoponera moelleri var. *splendens* Santschi 1929: 450; Brown 1958:228.

Gnamptogenys moelleri (Forel); Brown 1958:329; Kempf 1972:113; Kempf 1976:51.

Gnamptogenys teffensis (Santschi); Brown 1958: 329; Kempf 1972:115; Lattke 1990:24.

Diagnosis.—Slightly roughened costulae; pronotum with concentric costulae; posterodorsal mesosomal face with longitudinal costulae; subpetiolar process subquadrate, sometimes anteriorly projecting into a lobe.

Ecology.—Epigaeic forager of mostly lowland forested areas.

Comments.—Comparison of specimens determined as *G. moelleri* with *G. teffensis* forms reveal nothing beyond normal infraspecific variation. Santschi described *G.*

teffensis as a relative of *G. striatula* differing in gauge of costulation, pilosity, and size. The use of length vs. width of the funicular segments in separating *G. moelleri* from *G. teffensis* is useless as even in members of the same nest series the ratio will differ either way.

Specimens Examined.—ARGENTINA, 50 km S. Oran. BRAZIL, Amazonas: Fazenda Esteio, 80 km NNE Manaus, 2°25'S 59°46'W, 80m. COLOMBIA, Amazonas: 7 km N Leticia; Putumayo: 5 km S Mocoa, 610m; Meta: Río Guayabero, Isla Angostura, 279 m; Reserva La Macarena, 580m; Chocó: Finca Los Guaduales, 800m; Nariño: 28 km SE Mocoa, 510m. ECUADOR, Napo: Limoncocha, 250m; 59 km E Quevedo, Los Ríos, 2000m; PARAGUAY, Neembuca, Pilar. PERU, Panguana, 9°37'S 74°56'W, 220m; Puerto Maldonado, 260m. VENEZUELA, Barinas: 17 km SW Ciudad Bolivia, 8°04'N 70°48'W, 240 m.

Gnamptogenys mordax (Smith)

Ponera mordax F. Smith 1858:98.

Ponera nodosa Latreille 1802:217; Brown 1958: 228.

Ectatomma (*Gnamptogenys*) *mordax* (Smith); Emery 1896:49.

Gnamptogenys mordax var. *purensis* Forel 1912; Brown 1958:228.

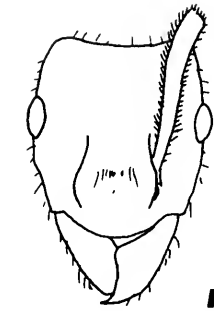
Gnamptogenys mordax (Smith); Mann 1922:3; Brown 1958:319; Kempf 1972:113; Kempf 1976:51; Lattke 1990:19.

Gnamptogenys mordax var. *sebastiani* Borgmeier 1937:220; Brown 1958:228.

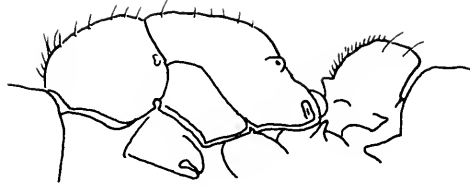
Diagnosis.—Mandibles subtriangular; declivitous propodeal face transversely costulate; gastric tergum II can vary from smooth to longitudinally costulate or costulate-rugose. Body very dark, brown, almost black; legs dark brown. Smaller individuals can be confused with *G. continua*.

Ecology.—A common dweller of humid forests.

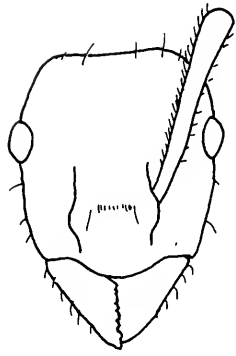
Comments.—Size (HW 1.08–2.08; WL 1.66–2.92 mm) and sculpture patterns of



56



57



58



59

Figs. 56–59. Frontal view of head, and lateral view of mesosoma and petiole. 56–57, *G. ilimani*; 58–59, *G. nigrivittrea*.

this widespread and timid species is quite variable.

Specimens Examined.—COSTA RICA, Heredia: 17 km N. Volcán Barba, 10°17'N 84°05'W, 880 m. GUYANA, Kaietur. MEXICO, Chiapas: Jetja. PERU, Panguana, 9°37'S 74°56'W, 220 m; Tingo María: Monsón Valley; 69 km E Tingo María, 1200m. VENEZUELA, Amazonas: Alto Río Siapa, 1°40'N 64°35'W, 600m.

Gnampptogenys nana Kempf

Gnampptogenys nana Kempf 1960b:422; Kempf 1972:113.

Paractatomma dina Kusnezov, 1969:35; Kempf 1978:35.

Diagnosis.—Head subquadrate, mandibles subtriangular with striae at base, clypeal lamella straight, no transverse mesosomal impressions, propodeal declivity with vertical costulae.

Ecology.—Unknown. Its nearest relatives, *horni* and *regularis* include beetles as a significant part of their diets, while *horni* also preys on ants.

Comments.—A rarely collected species, the specimen mentioned below is topotypic (MCZC).

Specimens Examined.—BRAZIL, São Paulo: Agudos.

Gnampptogenys nigrivittrea Lattke, new species (Figs. 58, 59)

Type Material.—Holotype worker: COLOMBIA, Valle: Reserva Forestal de Yotocó, 3°50'N 76°25'W, 42 km NNE Cali, 1100–1500 m, 6-I-84, W.P. MacKay, leg. No. 7221. Deposited in MIZA. Paratype: One worker with same locality data as holotype, deposited in LACM.

Worker.—Holotype (paratype) measure-

ments: HL 1.10 (1.10); HW 0.86 (0.82); ML 0.86 (0.82); ED 0.14 (0.12); SL 0.82 (0.84); WL 1.40 (1.36) mm; CI 0.79 (0.79); SI 0.95 (1.02); OI 0.16 (0.15). Head elongate; fairly parallel sided in frontal view; posterior margin slightly concave; clypeal lamella widest medianly, giving it a bluntly pointed aspect; eyes moderately protuberant. Mandibles triangular and shallowly costulate; no trace of mesometanotal suture; pronotum anterolaterally convex; declivitous propodeal face longitudinally costulate; metacoxal tooth triangular; node posteriorly inclined, in lateral view with a broadly convex anterior margin and a bluntly pointed apex which slightly overhangs the posterior margin, in dorsal view with longitudinal costulae; subpetiolar process is an anteriorly projecting lobe; anterior face of postpetiole with 3 transverse costulae, costulation longitudinal on dorsal face; postpetiolar sternum with distinct costulation; scape with few standing hairs and moderate amount of decumbent pilosity. Body black; antennae, legs, metapleural gland area, and gastric apex brown. Coxae very dark brown.

Female, Male.—Unknown.

Discussion.—The closest species to *G. nigrovitrea* is *G. brunnea*, but its well impressed mesometanotal groove, angulate anterolateral pronotal area and depressed apical and basal mandibular margins permit easy separation.

Etymology.—The species name is derived from the Latin adjectives for black, *nigra*, and for glassy, *vitrea*, and alludes to the black and shining sculpture.

Gnamptogenys perspicax Kempf and Brown

Gnamptogenys perspicax Kempf and Brown 1970: 316; Kempf 1972:114.

Diagnosis.—Eye slightly behind cephalic mid-length; scape longitudinally striate with abundant standing hairs; petiole node more or less evenly convex; postpe-

tiolar sternum with transverse costulae or rugae.

Ecology.—A millipede feeder found in humid forests.

Comments.—Apparently a sister species of *bispinosa*.

Specimens Examined.—ECUADOR, Pichincha, Estación Río Palenque (MCZC).

Gnamptogenys pilosa Lattke, new species (Figs. 51–53)

Type Material.—Holotype worker. COLOMBIA, Valle: Calima, Cañón El Pital, F. Castaño, leg. Deposited in MIZA. Paratypes: Three workers with same locality data as holotype. One deposited in each of the following: LACM, BMNH, MCZC.

The late Mr. F. Castaño kindly provided additional information about the type locality. The site is by a stream called Quebrada El Pital (tributary of Río Calima) in a gorge 900–1300 m above sea level. Approximate coordinates: 3°08'N 76°40'W. The site will soon be flooded due to construction of a dam. The specimens were found on leaf litter in a cloud forest.

Worker.—Holotype (paratypes) measurements: HL 1.44 (1.40–1.48); HW 1.20 (1.20–1.22); ML 0.54 (0.46–0.54); ED 0.28 (0.28–0.30); SL 1.46 (1.50–1.57); WL 2.00 (2.00–2.06) mm; CI 0.83 (0.81–0.86); SI 1.21 (1.25–1.28); OI 0.23 (0.23–0.25) $n=4$.

With head in frontal view, vertexal margin fairly straight, sides broadly convex; anterior clypeal margin convex, lamella well developed; eyes prominent on posterior one half of head; mandibles triangular, apical margin denticulate, dorsum striate; cephalic dorsum with longitudinal parallel striae, diverging posterad at vertex; 1–2 transverse striae parallel to occipital carina; anterior pronotal face transversely striate; dorsal mesosomal surface, including all of propodeum, longitudinally striate; striae curve around propodeal spiracles with no transverse striae between spiracles; lateral pronotal surface obliquely to transversely striate, striation

on pleura and lateral propodeal face parallel with dorsal striae; inner procoxal faces punctate, anterolaterally transversely striate; lateral faces of meso- and metacoxae weakly striate; metacoxa with well-developed tooth.

Petiolar node transversely striate, low; viewed laterally with convex anterior margin and concave posterior margin, apex overhanging; subpetiolar process with a projecting anterior lobe and subquadrate posteriorly; transverse striae anteriorly on gastric tergum, up to three-fourths length of tergum, rest of gaster longitudinally striate; anteroventral postpetiolar process prominent; sternite with longitudinal striation, diverging caudad; abundant erect to suberect hairs on body and extremities; abundant pilosity on coxae, propodeum, petiole, antennae and legs.

Queen, Male.—Unknown.

Discussion.—This is the hairiest of all *Gnamptogenys* species. On account of size, slender habitus, posteriorly inclined petiolar node, fine costulation, and abundant pilosity its nearest relatives appear to be *G. gracilis* and *G. ejuncida*. The sculpture of *ejuncida* is coarser, the pilosity is not as dense and the presence of erect hairs is considerably less. The break between the dorsal and declivitous propodeal faces is sharper in *G. pilosa*, giving it a more robust aspect. *G. gracilis* is an endemic from the Guiana Shield area, and has the postpetiolar sternal disc smooth and shining.

Etymology.—The species name is derived from the Greek word for hair: *pilos*.

***Gnamptogenys pittieri* Lattke**

Gnamptogenys pittieri Lattke 1990:21.

Diagnosis.—Sculpture with rough aspect; frontal lobes each with a median emargination; eyes protuberant and subglobular; propodeal spiracles mounted at the apex of protuberances.

Ecology.—Hypogeic leaf litter (including

bamboo) dweller of cloud forests of the Venezuelan Cordillera de la Costa.

Comments.—The series from near Tejerias differs from the type series in having the notch on the frontal lobes shallower, the propodeal spiracles on higher turrets, finer costulae on the anterior postpetiolar face and metacoxal spines more acute.

Specimens Examined.—VENEZUELA, Aragua: Pq. Nac. Henri Pittier, vic. Rancho Grande, 1500m; 17 km S Las Tejerias, 1300 m (MIZA).

***Gnamptogenys pleurodon* (Emery)**

Ectatomma (*Holcoponera*) *pleurodon* Emery 1896: 47.

Holcoponera emeryi Santschi 1929: 463 (nec Forel 1901).

Holcoponera vidua Santschi 1929:467; Brown 1958:229.

Gnamptogenys pleurodon (Emery); Brown 1958: 320; Kempf 1961:390; Kempf 1970:325; Kempf 1972:114; Lattke 1990:22.

Diagnosis.—Pronotum with concentric costulae; mesonotum with longitudinal costulae, sometimes surrounded by concentric costulae; anterior postpetiolar face with 3–4 transverse costulae and dorsal face with longitudinal costulae; metacoxal tooth acicular. Body dark brown, legs brown.

Ecology.—Kempf (1970) notes a nest preference for pre-existing cavities in plants. It is also a frequent forager on trees and shrubs. Usually found in lowland to premontane humid forests.

Comments.—An occasional specimens may have vertical costulation on the declivitous propodeal face, as in *striatula*, but the backwards tilt of the petiolar node and its brief anterior peduncle will identify *pleurodon*.

Specimens Examined.—BOLIVIA, Tumpasa. BRAZIL, Amazonas: Benjamin Constant, Fazenda Esteio, 80 km NNE Manaus, 80 m; Iriboca, Pirelli Plantation. COLOMBIA, Amazonas: 7 km N Leticia; Putumayo: 5 km S Mocoa, 610m. ECUADOR, Napo: Sushijindi; Tena, 400m. PERU, Ma-

dre de Dios: Estación Biológica Cocha Cashu, 400; Tingo María: Yurac, 108 km E Tingo María. SURINAM, Brownsberg Natuur Park. VENEZUELA, Amazonas, Alto Río Mavaca, 2°01'N 65°07'W, 200m; Bolívar, Auyán Tepui, Cañón del Diablo, Isla Ratón, 500m.

Gnamptogenys porcata (Emery)

Holcoponera porcata Emery 1896:48.

Holcoponera magnifica Santschi 1921:81. NEW SYNONYMY.

Gnamptogenys magnifica (Santschi); Brown 1959:320; Kempf 1972:113.

Gnamptogenys porcata (Emery); Brown 1958:320; Kempf 1972:114; Lattke 1990:23.

Diagnosis.—Costate species, median longitudinal costae on pronotum inscribed anteriorly by transverse costae; postero-dorsal mesosomal sculpture variable: concentric ovaloids with longitudinal or transverse orientation, or with longitudinal costae inscribed within whorls; piceous body with ferruginous legs.

Ecology.—A dweller of premontane to montane humid forests. J. Longino (pers. comm.) found an incipient nest in *Cecropia insignis*. One nest midden contained mostly the remains of beetles: scolytids, bostrichids, curculionids, besides isopods. Nests from one population (Venezuela, Táchira) consistently had their brood chambers irregularly wall-papered with the remains of pupal cocoons.

Comments.—Santschi described *magnifica* as close to *porcata* but differing in its larger size and the transverse costulae on the posterior dorsal mesosoma. Brown (pers. comm.) studied the *magnifica* type in 1963 and noted it was "very close" to *porcata* with the former slightly larger and with a higher, thinner node as seen laterally. Specimens in the USNM from Bolivia collected by Mann during 1956 bear anonymous *Holcoponera magnifica* determinations. The study of series from Venezuela representing several colonies from different populations show great variability for dorsal mesosomal sculpturing. Size differ-

ences between the two forms are no more than infraspecific. One Honduran worker has a wide, lobe-like subpetiolar process.

Specimens Examined.—BOLIVIA (no other data); COLOMBIA, Antioquia: Río Porce, 1020m; Cundinamarca: above Tena, 1300–1600 m; Valle: 3.2 km above Río Agua Clara, old Cali-Buenaventura rd; Río San Juan (tributary of Río Digua), vic. Queremal, 1300m; Municipio Buenaventura, 650 m. COSTA RICA, Río Toro Amarillo, vic. Guapiles, < 40 m; Heredia: 10°19'N 84°43'W, 800m. ECUADOR, Pichincha: Tinalandia, 16 km SE Sto. Domingo de los Colorados, 680m. HONDURAS, 14 km S La Ceiba; Lombardia. VENEZUELA, Táchira: vic. Siberia, 39.7 km WNW San Cristóbal, 1200m; Trujillo: 15 ESE Boconó, 1160m.

Gnamptogenys rastrata (Mayr)

Ectatomma (*Parectatomma*) *rastrata* Mayr 1866:89.

Gnamptogenys trigona Emery 1905:114; Brown 1958:321; Kempf 1972:116. NEW SYNONYMY.

Gnamptogenys rastrata (Mayr); Brown 1958:322; Kempf 1972:114; Kempf 1976:52.

Diagnosis.—Antennal scapes surpass vertexal margin by no more than their apical width; triangular and edentate mandibles with a varying degree of costulae and rugae; small tubercle-like propodeal teeth next to conspicuous spiracles which are slightly elevated above rest of surrounding cuticle; postpetiolar sternum with median longitudinal smooth and shining areas.

Ecology.—Captured in wet forests, including montane areas. A millipede feeder.

Comments.—*G. trigona* was separated from *rastrata* on account of differences in the gauge and form of the costulation, as well as size. Variability of mandibular sculpture on basal flange and dorsum is nothing beyond infraspecific. The sculpture on the node as seen dorsally can vary from concentric costulae, with transverse or longitudinal costulae in the middle, or

completely transverse. Costulae transverse on anterior petiolar node face. Brown (1958:321) discusses the differences in size, costulae counts, length vs. width of node, subpetiolar process shape and variability of sculpture on node between the specimens of *G. rastrata* and *G. trigona* he examined. As more specimens became available the gaps were bridged. The petiolar node can be wider than long or the opposite. Size range is HL 0.74–0.90; WL 1.10–1.28 mm.

Specimens Examined.—Brazil, Rio de Janeiro: Jussaral; São Paulo: São Bernardo do Campo; Nova Teutonia, 27°11'S 52°23'W, 300–500m (MCZC).

Gnamptogenys regularis (Mayr)

Gnamptogenys regularis Mayr 1870:965; Mann 1922:3; Brown 1959:229, 319; Kempf 1972:114; Lattke 1990:23.

Gnamptogenys rimulosa var. *splendida* Pergande 1896:871; Brown 1959:229.

Gnamptogenys fiebrigi Forel 1909:253; Brown 1958:229.

Diagnosis.—Declivitous propodeal face abruptly separated from dorsal face, superolaterally with small angulate lobes; metacoxal tooth apically rounded and not triangular; dark brown body, testaceous legs.

Ecology.—J. Longino (pers. comm.) reports observing a short linear column of workers walk to an apparent nest entrance on the ground. He excavated it before any activity had begun and found a small colony of *Pseudomyrmex boopis*. The related *G. horni* has a dietary preference for ants and beetles (Lattke, 1990). One specimen was removed from the stomach of a *Tamandua tetradactylus*.

Comments.—The degree of transverse costulation on the anterior nodal face has traditionally been used to separate this species from *horni*, but as additional material accumulated it became impossible to rely on the character. Transverse costulation can be totally absent or occupy all of the anterior nodal face. Females tend to

have the anterior nodal face totally transversely costulate. This was noted for one specimen by Mayr (1871:965) who concluded it was not normal and that a female with longitudinal costulae would eventually be found. The longitudinal costulae on the sides of the mesosoma do not curve onto the declivitous propodeal face. The type of *splendida* was examined in the CASC.

Specimens Examined.—ARGENTINA, Tintina. BRAZIL, Amazonas: Reserva Ducke, vic. Manaus; Maturaca. COLOMBIA, Magdalena: 4 km N San Pedro, 10°57'N 74°03'W, 550 m. COSTA RICA, Alajuela: vic. Volcán Arenal, 10°29'N 84°44'W, 550 m. Heredia: 10°20'N 84°04'W, 500 m; Península de Osa: Sirena, 8°28'N 83°35'W, 50m; Puntarenas: Res. Biol. Carará, 9°47'N 84°36'W, 500m; vic. Guapiles, Río Toro Amarillo. BRAZIL, Goiás: Anápolis; São Paulo: Holambra; Agudos; Distrito Federal: Deodoro; Amazonas: Maturaca; Minas Gerais: Carmo da Cachoeira; Bahia: Salvador. ECUADOR, Pichincha: Río Palenque, Centro Científico; Santo Domingo de los Colorados; Pichilingue: Los Rios. GUIANA, (NY Quarantine Stn.). MEXICO, Tepic; Veracruz: 10 km NNW Sontecomapán, 200m. PERU, Tingo María: Valle del Monsón; Junín: Colonia Perene, Río Perene, 18 km NE La Merced; Puerto Maldonado, 260 m. VENEZUELA, Sucre: El Rincón, 10°36'N 63°12'W, 100 m; Guárico: Hato Masaguaral.

Gnamptogenys reichenspergeri (Santschi)

Acanthoponera (*Anacanthoponera*) *reichenspergeri* Santschi 1929:274.

Gnamptogenys reichenspergeri (Santschi); Brown 1958:324; Kempf 1972:114.

Diagnosis.—Head in frontal view with concave vertexal margin, vertex smooth and shining; anterior face of postpetiole and median disc of gastric tergum II smooth and shining; metacoxal spine ab-

sent and declivitous face of propodeum with small superolateral lobes, spiracles lateral and not elevated; metanotal suture absent.

Ecology.—From leaf-litter samples of humid forests.

Comments.—A rarely collected ant, its nearest relative is apparently *relicta*.

Specimens Examined.—BRAZIL, Jussara: Angra dos Rios (MCZC). VENEZUELA, Amazonas: Cerro Ya-pakana (LACM).

Gnamptogenys relicta (Mann)

Rhopalopone relicta Mann 1916:403.

Holcoponera relicta (Mann); Brown 1957:491.

Gnamptogenys relicta (Mann): Brown 1958:229; Kempf 1972:114; Wheeler & Wheeler 1975: 119.

Diagnosis.—Mandibles, vertex and anterior postpetiolar face smooth and shining, occiput sometimes with very faint transverse costulae; last 3 antennal segments form vague club; declivitous propodeal face with transverse costulae, propodeal spiracles elevated above rest of cuticle; pronotal suture present but fine, metanotal suture well impressed, breaking sculpture; no anterolateral lobes on declivitous propodeal face; metacoxal spine present.

Ecology.—Sifted from leaf litter in rain forests.

Comments.—The degree of effacement of sculpture, and size can vary considerably. S. Cover reports a specimen from the N. Range of Trinidad.

Specimens Examined.—BRAZIL, Amazonas: Rio Taruma, High Falls; Benjamin Constant; Ponta Negra, N of Manaus; 66 km N Manaus on Carcari road. COLOMBIA, Amazonas: 7 km N. Leticia. SURINAM, Raleigh Vallen-Voltzberg Res., Voltzberg Camp, 90m. VENEZUELA, Bolívar: 49 km ESE Tumeremo, 7°28'N 61°06'W, 200 m.

Gnamptogenys rimulosa (Roger)

Ponera rimulosa Roger 1861:18.

Gnamptogenys rimulosa (Roger); Brown 1958:324; Kempf 1972:114.

Diagnosis.—Mandibles with small basal patch of costulae, rest smooth and shining; metacoxa with broad, basal lobe; petiolar node longitudinally costulate throughout; postpetiolar sternum smooth and shining.

Ecology.—Unknown.

Comments.—This species seems to be particularly close to *G. regularis*. Even though *regularis* workers lack the small laterobasal costulate area on the mandibles, females have it; there is a slight depression of the posterior mesosomal dorsum, vestigial propodeal lobes and totally longitudinal costulae on the node.

Specimens Examined.—BRAZIL, Santa Catarina: Nova Teutonia: 27°11'S 52°23'W, 300–500m.

Gnamptogenys schmitti (Forel)

Emeryella schmitti Forel 1901:334; Wheeler & Wheeler 1952:127.

Emeryella schmitti minor Wheeler 1936:195; Brown 1958:229.

Gnamptogenys schmitti (Forel); Brown 1958:330; Kempf 1972:114.

Diagnosis.—Very broad head, in frontal view, and striking elongate mandibles without denticles; striae on anterior nodal face transverse, slightly effaced laterally; striae on metanotum and propodeum transverse; gastric sternum II smooth and shining.

Ecology.—A predator of millipedes whose range has shrunk considerably this century due to massive deforestation on Hispaniola.

Comments.—This species represents an extreme in the development of falcate mandibles within the genus (Brown 1958: 215), but probably represents a development independent of the *banksi* subgroup species. The type series in the MCZC was examined.

Specimens Examined.—HAITI, Diquini.

Gnamptogenys semiferox Brown

Gnamptogenys semiferox Brown 1958:324; Kempf 1972:114.

Diagnosis.—Body with abundant coarse punctation, especially on head; mandibles with about six denticles and projecting basal lobe; anterior clypeal margin convex; declivitous propodeal face longitudinally costulate.

Ecology.—A millipede hunter known from rain forests between 900–1200 m on Hispaniola. Also suffering from habitat shrinkage due to deforestation.

Comments.—Even though it shares the lack of metacoxal spines and elongate mandibles with *schmitti*, it does not seem to be closely related to it. Its mandibles are different, including in cross section: shining and longitudinally rugulose, as opposed to opaque and striate in *schmitti*.

Specimens Examined.—DOMINICAN REPUBLIC, Mt. Diego de Ocampo, 3–4000 ft (Paratype).

***Gnamptogenys siapensis* Lattke,**
new species
(Figs. 62, 63)

Type Material.—Holotype worker. VENEZUELA, Amazonas: Alto Río Siapa, 1°40'N 64°35'W, 600 m, 4-II-89, J. Lattke, leg. Sifted leaf litter sample. The specimen was caught in an area occasionally flooded during the rainy season. Deposited in MIZA.

Worker.—HL 1.13; ML 0.44; HW 1.00; ED 0.25; SL 0.97; WL 1.60 mm; CI 0.89; SI 0.97; OI 0.25.

Cephalic dorsum with fine longitudinal costulae; eyes placed behind midlength; clypeal lamella anteriorly straight and laterally bluntly angulose; mandibles smooth and shining, subtriangular with apical and basal margins joined through broad convexity; scapes smooth and shining, surpassing vertexal margin, antennal bullae partially visible beneath frontal lobes; costulae longitudinal throughout mesosomal dorsum, propodeal declivity and petiolar node; promesonotal and mesometanotal sutures weakly impressed; mesometapleural suture well impressed; petiolar node more or less as long as wide, in lat-

eral view subquadrate; subpetiolar process subquadrate, with angulate ventral corners; postpetiolar sternum medially smooth and shining and with lateral longitudinal costulae; tibiae and femora smooth and shining; metacoxae with basal triangular lobe, dorsally transversely costulate and laterally mostly smooth and shining; abundant long suberect and subdecumbent hairs on body. Color ferruginous.

Queen, Male.—Unknown.

Discussion.—This species is quite near to *lucaris* and the differences between the two species may be infraspecific: in *lucaris* the petiolar node dorsum is evenly convex, the metacoxal tooth is broadly triangular and the subpetiolar process has acutely pointed angles. Due to the great differences that separate the range of the two species, the apparent endemism of some *Gnamptogenys* to southern Brazil, and the scarcity of material, it seemed prudent to separate the forms until more specimens are available.

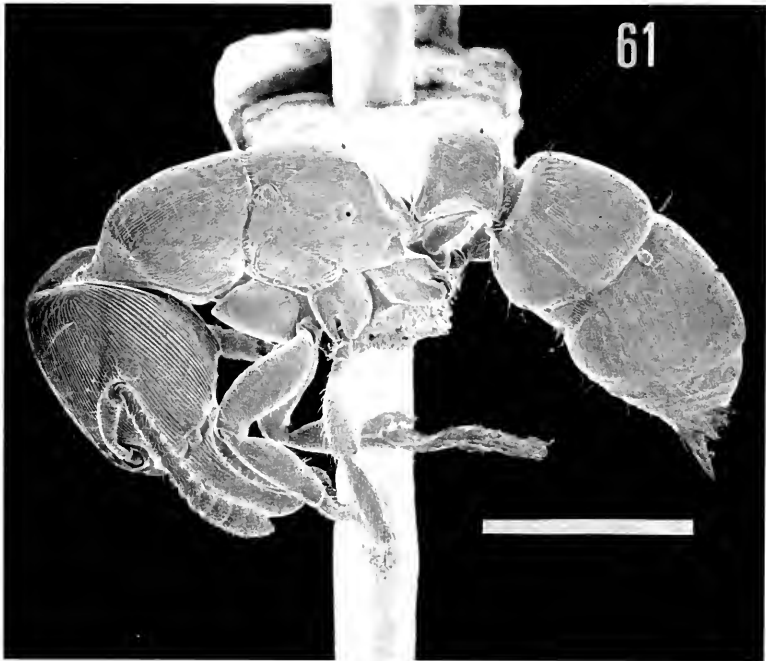
Etymology.—The species name alludes to the type locality.

***Gnamptogenys stellae* Lattke,**
new species
(Figs. 60, 61)

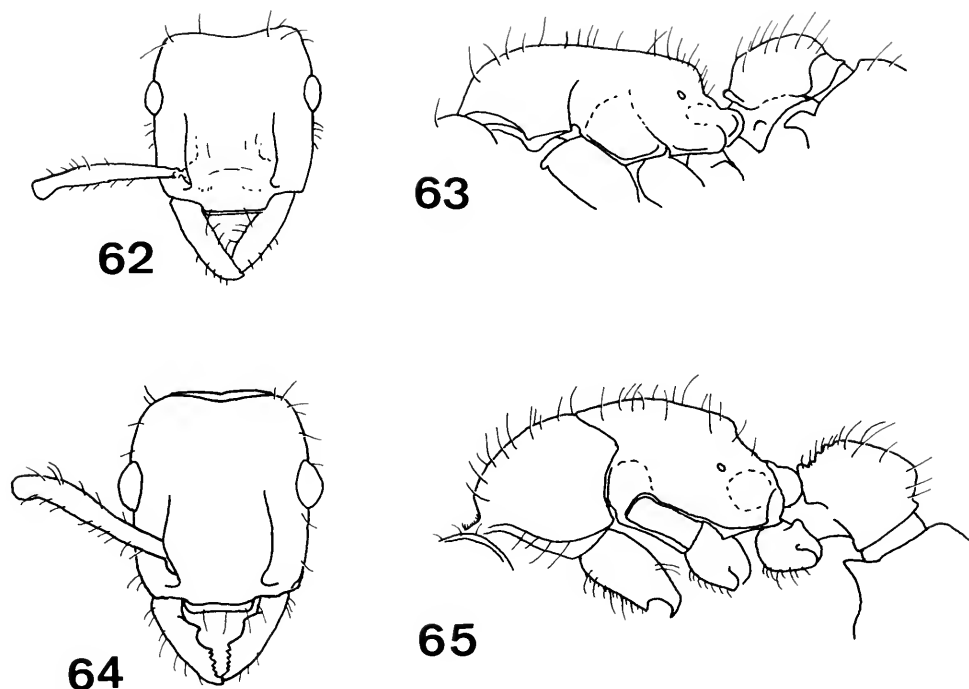
Type Material.—Holotype worker. COSTA RICA, Estrella Valley, April, 1924, W.M. Mann, leg. Deposited in USNM.

Worker.—Holotype measurements: HL 1.18; ML 0.57; HW 1.06; SL 0.65; ED 0.13; WL 1.55 mm; CI 0.90; SI 0.61; OI 0.12.

Head elongate, in frontal view with concave vertexal margin, more or less parallel sided with eyes at about midlength; clypeal lamella gradually projects forward from sides and is medially weakly emarginate; mandibles almost linear and with a double row of low tubercles on apical border, dorsally and laterally smooth and shining with sparse punctae, basally with small area of longitudinal costulae; scapes smooth and shining, dorso-ventrally compressed, bent at basal one-fourth and



Figs. 60–61. Micrographs of *G. stellae*. 60, head, scale bar = 0.5 mm; 61, body, scale bar = 1.0 mm.



Figs. 62–65. Frontal view of head and lateral view of mesosoma and petiole. 62–63, *G. siapensis*; 64–65, *G. volcano*.

thickest just apicad of midlength; cephalic dorsum with longitudinal striae, diverging posterad at vertex, gula mostly longitudinally striate, weakly diverging posterad; occipital margin glabrous.

Anterior pronotal face and collar with transverse striae; longitudinal striae on mesosomal dorsum and propodeal declivity, slightly shallower on metanotum and dorsal propodeal face; promesonotal suture very lightly impressed, metanotal groove markedly impressed and interrupting longitudinal striae. Mesosomal sides longitudinally striate, except for oblique striae on anepisternum; propodeal spiracle round and slightly raised above rest of integument; procoxae anteriorly and anterolaterally smooth and shining, posterolaterally striate; mesocoxae with dorsal transverse striae that are effaced posteriorly; metacoxae with transverse striae and low dorsobasal swelling; tibia and femora smooth and shining; anterior

petiolar node face smooth and shining, laterally with weakly effaced longitudinal striae, dorsally diverging posterad; node wider posterad than anterad; petiole in lateral view slightly pedunculate, anteriorly slightly concave, dorsally slightly convex, posterior face dropping sharply; subpetiolar process anteriorly projecting with convex anterior border and posteriorly sinuous; gastric terga I and II with longitudinal striae, effaced towards posterior margin of tergum II. Gastric sterna I and II smooth and shining; pilosity sparse, a row of stout hairs present along apical mandibular order, few standing hairs on posterior cephalic dorsum, pronotum and gaster. Body reddish brown; mesosomal dorsum and head darker brown, leg and antennae ferruginous.

Queen, Male.—Unknown.

Discussion.—The median anterior projection of the clypeal lamella is unique among the extant species of the mordax

group. This species seems to occupy an intermediate position between *G. continua* and *G. horni*. The combination of clypeal configuration, small eyes, subfalcate mandibles, glabrous occiput, mesometanotal suture and very brief petiolar peduncle point to this placement.

Etymology.—The species epithet is derived from the Latin word for star, *stella*, and alludes to the type locality.

Gnamptogenys striatula Mayr

Gnamptogenys striatula Mayr 1883:32; Mann 1916:404; Brown 1959:327; Kempf 1970:325; Kempf 1972:115; Kempf 1976:52; Lattke 1990:23.

Holcoponera curtulum Emery 1896:47; Forel 1899:7. NEW SYNONYMY.

Holcoponera obscurum Emery 1896:48; Luederwalt 1926:238; Santschi 1929:442.

Holcoponera curtula var. *stolli* Forel 1899:7; Brown 1958:228.

Holcoponera brasiliensis Emery, 1902:181; Brown, 1958:229.

Holcoponera striatula obscura var. *angustiloba* Forel 1908:341; Luederwalt 1926:237; Brown 1958:229. Unavailable.

Holcoponera striatula obscura var. *simplicoides* Forel 1908:341; Luederwalt 1926:328. NEW SYNONYMY. Unavailable.

Holcoponera striatula obscura var. *angustipleura* Forel 1908:342; Brown 1958:229. Unavailable.

Holcoponera curtula var. *paulina* Forel 1908:342; Brown 1958:229.

Holcoponera curtula var. *vollenweideri* Forel 1912:33; Santschi 1929:453; Brown 1958:229.

Holcoponera striatula (Mayr); Luederwalt 1926:237; Santschi 1929:442; Wheeler and Wheeler 1952:123.

Holcoponera striatula var. *antillana* Santschi 1929:444; Brown 1957:490.

Holcoponera rustica Santschi 1929:446. NEW SYNONYMY.

Holcoponera wheeleri Santschi 1929:448. NEW SYNONYMY.

Holcoponera brasiliensis var. *pernambucana* Santschi 1929:452; Brown 1958:229.

Holcoponera brasiliensis var. *calcarata* Santschi 1929:452; Brown 1958:229.

Holcoponera brasiliensis var. *mayri* Santschi 1929:453; Brown 1958:230.

Holcoponera brasiliensis simplicoides Santschi 1929:45.

Holcoponera brasiliensis simplicoides var. *hybrida* Santschi 1929:455; Brown 1958:229. Unavailable.

Holcoponera emeryi var. *recta* Santschi, 1929:465; Brown, 1958:229. NEW SYNONYMY.

Holcoponera regularis arcuata Santschi 1929:457; Brown 1958:227; Kempf 1972:112. NEW SYNONYMY.

Holcoponera regularis Santschi 1929:457 (nec Mayr 1970); Brown 1958:227.

Holcoponera wasmanni Santschi 1929:466. NEW SYNONYMY.

Holcoponera wasmanni var. *isthmica* Santschi 1929:467.

Gnamptogenys arcuata (Santschi); Brown 1958:227, 237; Kempf 1972:112.

Gnamptogenys curtula (Emery); Brown 1958:227, 327; Kempf 1972:112.

Gnamptogenys simplicoides (Santschi); Brown, 1958:229, 327; Kempf, 1972:114.

Gnamptogenys rustica (Santschi); Brown, 1958:229, 327; Kempf, 1972:114.

Gnamptogenys wasmanni (Santschi); Brown 1958:229, 238; Kempf 1972:116.

Gnamptogenys wheeleri (Santschi); Brown 1958:230, 238; Kempf 1972:116.

Diagnosis.—Pronotal costulae semicircular; dorsoposterior mesosomal costulae longitudinal and slightly diverging caudad; mesometanotum sometimes with semicircular costulae; triangular metacoxal teeth; body dark brown.

Ecology.—A generalist epigaeic forager of humid forests. See Lattke (1990). A mite was found on the anterolateral petiolar side of one specimen from Beni, Bolivia.

Comments.—This widespread, common, and fairly variable ant has been the object of a lengthy synonymic list. Most of the names were based upon differences in size, gauge of costulation, and the shape of the subpetiolar process and the mesopisternal lobe. These size differences are all normal for the species. One can recognize coarsely costulate and finely costulate specimens, as well as intermediate forms. The finely costulate ants can be found in several places: s. Brazil, Argentina, Guia-

na, Costa Rica, Jamaica and Hispaniola. Occasional series can be found that have transverse costulae on part or all of the propodeal declivity; this condition is not frequent on the finely costulate forms. Several series from Bolivia have a long anterior slope of the node, which approaches the condition in *pleurodon*. The use of the subpetiolar process in the separation of species is of limited value as a variation from subquadrate to anteriorly projecting lobe can be found in series from the same population or even nest. Brown (1957:489) already discussed the futility of using the mesepisternal lobe.

Specimens determined as *G. curtula* by Brown for the 1958 revision are *G. striatula*, and so are several specimens determined as *H. wasmanni* var. *isthmica*. Specimens labelled as type series of *H. emeryi recta* were studied in the USNM and found to be conspecific with *striatula* and not with *G. pleurodon*. I was able to examine two *G. striatula* syntypes in the BMNH. Bill Brown generously shared the notes he took during his study of the following Santschi types in 1963: *H. regularis*, *H. regularis* v. *arcuata*, *H. rustica*, and *H. wheeleri*. He concluded that they are all the same species. He also wrote that these specimens plus additional types and specimens he studied (*H. striatula* v. *antillana*, v. *angustipleura*, *H. wasmanni*, *H. wasmanni* v. *isthmica*, *H. brasiliensis* v. *calcarata*, v. *mayri*, *H. curtula* v. *paulina* (det. Santschi)) perhaps could be separated into two species using the subpetiolar process. But as already has been mentioned, this process has proven to be an unreliable character for species determination in this group.

Material Examined.—ARGENTINA, Salta: El Rey; Misiones: Puerto Iguazu. BOLIVIA, Beni: Blancaflor. BRAZIL: Pará: Tukurul; São Paulo: Reserva Caraguatatuba, 40–80 m; Rio Grande do Sul: Caixa do Sul, Nossa Senhora da Saúde; Ceará: Maranganape Mts. COLOMBIA, Meta: Reserva La Macarena, Río Guayabero, 270m; Quebrada Chirijara, Villavicencio, 1400m;

Cundinamarca: 81 km de Bogotá; Fusagasugá; Valle: Sevilla; Cali, 90m. COSTA RICA, Hacienda La Pacífica, 50m; Limón: Finca La Lola, Siquerres; Heredia: Finca La Selva; Puntarenas: 6 km SW Monteverde, 10°16'N 84°50'W, 900m. DOMINICAN REPUBLIC, Clarke Hall. ECUADOR, Napo: Limoncocha, 250m; Sushijindi: Sucuá: 1500m. JAMAICA, St. Ann, Cedar V., 760m; Westmor. bog, 460m. EL SALVADOR, 6,4 Km N Quetaltepec. MARTINIQUE, (no other data). MEXICO, María Madre; Michoacán: 8 km SW Tiquicheo, 430m; Consequina slope; Sinaloa: Mazatlán; Veracruz: Lago Catemaco, 250m; 5 km S Cuernavaca; Chiapas: 8 km NE Huixtla, 225m. PERU, Panguana, 9°37'S 74°56'W, 220 m; Puerto Maldonado, 260m. PUERTO RICO, 49 Carr. 186, km 13.2, Río Grande, Humacao. VENEZUELA, Amazonas: Alto Mavaca, 2°01'N 65°07'W, 200m; Táchira: Las Cuevas, 7°48'N 71°46'W, 200 m.

Gnamptogenys strigata (Norton)

Holcoponera strigata Norton 1871:4.

Holcoponera concentrica Mayr 1870:964; Emery 1891:167.

Holcoponera simplex Emery 1896:46; Kempf and Brown 1968:90.

Holcoponera satzgeri Forel 1908:39; Brown 1957:490.

Holcoponera simplex spuria Forel 1908:39; Brown 1957:490.

Holcoponera simplex foreli Santschi 1929:460; Brown 1957:490.

Gnamptogenys simplex (Emery); Brown 1958:229.

Gnamptogenys strigata (Norton); Brown 1958:329; Kempf 1958:115; Kempf and Brown 1968:90; Kempf 1972:115; Billen 1986:168.

Diagnosis.—Roughly costate; anterior postpetiolar surface fairly flat and with 3–4 transverse costae; abundant long, subdecumbent and suberect hairs on body.

Ecology.—A dweller of wet montane transandean forests, commonly taken in leaf litter samples.

Comments.—Aside from aspects covered by Kempf & Brown (1968), other charac-

ters that vary are the size of the propodeal spiracle, costulation of the propodeal declivity and the shape of the node.

Specimens Examined.—COLOMBIA, Valle: Pance, 1700m; Reserva Forestal de Yotocó. COSTA RICA, Monteverde: 1520m; Puntarenas: 1300–1580m; Alajuela: Río Peñas Blancas, 800–880m; Heredia: 17–12 km N Volcán Barba, 880–1420m; San José: 2 km E San Gerardo, 9°27'N 83°43'W, 1440m. GUATEMALA, Sepacuite. MEXICO, Chiapas: Ocosinga; 19 km NW Ocozocoautla, 975m; Veracruz: 5 km N Cuilhuac.

***Gnamptogenys sulcata* (Smith)**

Ectatomma sulcatum F. Smith, 1858:99.

Ponera tornata Roger 1861:15. NEW SYNONYMY.

Gnamptogenys lineata Mayr 1870:965; Brown 1958:229.

Gnamptogenys sulcata var. *cearensis* Forel 1912:33; Brown 1958:229

Gnamptogenys sulcata var. *nitens* Mann 1916:407; Brown 1958:229.

Gnamptogenys ypirangensis Borgmeier 1928:229.

Gnamptogenys sulcata bufonum Weber 1938:208; Brown 1958:229.

Gnamptogenys sulcata (Smith); Brown 1958:329; Kempf 192:115; Lattke 1990:24.

Gnamptogenys tornata (Roger); Mann 1922:3; Brown 1958:319, 329; Kempf 1968:378; Kempf 1972:116; Lattke 1990:25.

Diagnosis.—Mandibles subtriangular; dorsal mesosomal costulae convergent caudad and transverse on declivitous propodeal face; metacoxal tooth absent, at most present as very small tubercle or short lobe; very variable color: mesosoma black to light brown, frequently head, gastric apex and posterior margin of gastric tergum II darker than rest of body. Legs antennae, and mandibles light to dark brown.

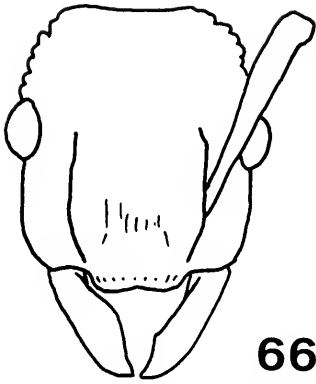
Ecology.—Used as prey by *Dendrobates histrionicus*. See Lattke (1990).

Comments.—Color is of no help in separating the aforementioned forms, except at an occasional local level. Brown (1958) recognized these difficulties and made it

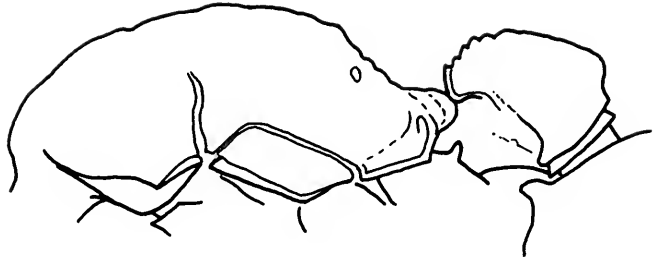
clear the situation would need further study. Variation has been observed in size and shape of the subpetiolar process, mandibular width, and relative size of the eyes. The node can project posteriorly and approach the condition in *acuminata* but does not become acutely pointed. Even though the propodeal declivity is commonly transversely costulate, it can sometimes have oblique or even longitudinal costulae.

I examined the *sulcata* type in the BMNH found it to have transverse costulae on the posterior nodal face. Roger's description includes a key character that points to *tornata*'s synonymy with *sulcata*: "The petiole, as in *rimulosa*, is concentrically costulate, with the smallest circle or oval in the middle of the dorsum, gradually becoming larger." This I have interpreted as meaning that the costulation on the posterior face of the petiole is transverse. My examination of Mann's *nitens* type reveals transverse costulation on the posterior petiolar face, longitudinal costulae on the declivitous propodeal face and very low triangular metacoxal teeth. Borgmeier's *ypirangensis* is described with transverse costulae on the posterior nodal face. Dr. Ivan Löbl of the MHNG kindly examined the *cearensis* type and reported transverse costulae on the posterior nodal face. Dr. Max Fischer of the NHMV graciously examined the types of *lineata* and reported transverse costulation. What could constitute a separate species are specimens from the Amazonas Basin (MUSP) that are black with yellow mandibles and are considerably larger than the average *sulcata*. But in the midst of so much variability it is prudent to await the accumulation of additional evidence before coining a name for a few specimens.

Specimens Examined.—BELIZE, Caves Branch. BOLIVIA, Rosario. BRAZIL, Amazonas: 24 km NE Manaus, Ig. Marianil, Rio Branco Rd.; Independencia: Parahyba; Pará: Rio Xingú (Cachoiera do Espelho); 10 km N Tucuru; Porto Velho: Rio Ma-



66



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Figs. 66–67. *G. transversa*. 66, frontal view of head; 67, lateral view of mesosoma and petiole.

deira. COLOMBIA, Casanare: (no other data); Magdalena: 12 km ESE Minca, 11°08'N 74°06'W, 780m; Parque Tayrona, Pueblito, 300m; Meta: Vista Hermosa; S Villavicencio, Caño El Buque, 480m; Nariño: La Guayacana; Sucre, Est. Primates Inderena; Valle: 64 km E Buanventura, 570m. COSTA RICA, Sirena: Península de Osa, 8°28'N 83°35'W, 50m; Pq. Nac. Braulio Carrillo, 500m; Península de Osa, Pq. Nac. Corcovado, San Pedrillo, 0–100m; Puntarenas: 5 km N Ciudad Neily, 780m; Heredia, 10°20'N 84°04'W, 500m. ECUADOR, Estación Río Palenque; Pichincha: Tinalandia, 16 km SE Santo Domingo de los Colorados. GUATEMALA, Escuintla. HONDURAS, Ola, 18 km NE Catcamas, 370m. MEXICO, Veracruz: Lago Catemaco, 350m; Los Tuxtlas, 10 m NNW Sontecomapán, 200m; trail above Presidio, 305–490m; Córdoba. PANAMA, Barro Colorado. PERU, Tingo María: Yurac, 107 km E Tingo María; Madre de Dios: Est. Biol. Cocha Cashu, 400m; Río Tambopata Res., 20°50'S 69°20'W, 290m; Huanuco: Cueva de la Lechuzas, 6 km W Tingo María; Cueva de la Boca del Lobo, 710m, 69 km W Tingo María. VENEZUELA, Amazonas: Alto Mavaca, 2°02'N 65°06'W, 250; Río Baría, 0°50'N 66°10'W, 140m.

***Gnampptogenys tortuolosa* (Smith)**

Ponera tortuolosa F. Smith 1858:99.

Gnampptogenys tortuolosa var. *quitensis* Forel 1921:133; Brown 1958:230.

Ectatomma (*Gnampptogenys*) *tortuolosum* (Smith); Emery 1896:51; Mann 1916:406; Wheeler and Wheeler 1952:134.

Gnampptogenys tortuolosa (Smith); Brown 1958:230; Kempf 1961:492; Kempf 1970:325; Kempf 1972:116; Lattke 1990:25.

Diagnosis.—Mandibles subtriangular; clypeal lamella laterally angular and medianly straight to softly concave; propodeum with transverse costulae; coxal tooth small sometimes shaped as a short lobe; tibiae, femora and scapes smooth and shining. Piceous body; legs and antennae ferruginous.

Ecology.—Found nesting in rotten wood in humid forests and foraging in grassy or weedy areas.

Comments.—Very constant in sculpture and color.

Specimens Examined.—BRAZIL, Roraima: 64 km S Boa Vista. COLOMBIA, Amazonas: Trocha Buenos Aires; Meta: 8 km w Villavicencio; Mesetas, La Uribe, 720m; Serranía La Macarena. ECUADOR, Sucua. GUIANA, Kartabo; Bartica; Rupupuni: Apoteri, 4°05'N 58°35'W, 100m. VENEZUELA, Amazonas: Alto Río Siapa, 1°05'N 58°35'W, 600m; Alto Río Mavaca, 2°01'N 65°07'W, 200.

***Gnampptogenys transversa* Lattke,**
new species
(Figs. 66, 67)

Type Material.—Holotype worker: PANAMA, Bocas del Toro, Fortuna-Chirigui

Grande rd., 8°47'N 82°12'W, 12/14-VII-78, 1050m, D.M. Olson (523), leg. Premontane rainforest sifted leaf litter. Deposited in MCZC.

Worker.—Holotype measurements: HL 1.30; HW 1.10; ML 0.70; ED 0.28; SL 1.04; WL 1.92 mm; CI 1.18; SI 0.95; OI 0.25.

Head in frontal view with rectangular, elongate head: sides broadly convex, posterior margin slightly concave; clypeal lamella relatively long, medianly slightly concave and laterally rounded; eyes moderately prominent. Costulae on head principally longitudinal, slightly convergent anterad, costulae between eyes and frontal lobes curving into depression laterad of antennal sclerite. Mandibles triangular with blunt denticles and relatively long basal broader, rugulose with piligerous punctae. Scapes shining and slightly rugulose, barely passing posterior edge. Mesosoma dorsally with longitudinal costulae from pronotum to dorsum of propodeum, declivity with transverse costulae; promesonotal suture visible as a brief transverse depression. Laterally with longitudinal costulae throughout. Anepisternal flange well-developed along anterior third; katapisternum well-defined, anepisternum not as well-defined. Petiole laterally subcylindrical, costulae longitudinal/oblique, ventral process is an anteriorly projecting lobe. Petiole in dorsal view wider posteriorly than anteriorly, costulae form concentric arches: transverse in oblique-anterior view and longitudinal in posterior view. Gastric dorsum with longitudinal costulation, postpetiolar sternal disc smooth and shining. Transverse costulae on forecoxa, metacoxa with a parallel-sided denticle with a rounded apex.

Antennae, tibiae, femora with no pilosity, only decumbent to suberect hairs and sparse punctulae. Body brown, legs ferruginous brown.

Female, Male.—Unknown.

Discussion.—This species is very close to *hartmani* but *hartmani* has longitudinal costulae on the propodeal declivity; mostly

smooth and shining mandibles; dorsum of petiole with mostly longitudinal striae; longitudinal striae on the postpetiolar sternum; eyes not as prominent, and scapes with more defined striae and rugulae.

Etymology.—The name alludes to the transverse costulae on the propodeal declivity.

Gnamptogenys triangularis (Mayr)

Ectatomma (Gnamptogenys) triangularis Mayr 1887:544.

Gnamptogenys triangularis (Mayr); Emery 1905: 113; Kusnezov 1954:34; Brown 1958:323; Kusnezov 1962:236; Brown 1958:230 321.

Ectatomma (Parectatomma) triangularis richteri Forel 1913:203; Luederwalt 1926:236; Brown 1958:230 321.

Ectatomma (Parectatomma) aculeaticoxae Santschi 1921:82; Wheeler and Wheeler 1952:133. NEW SYNONYMY.

Gnamptogenys aculeaticoxae (Santschi); Brown 1958:227, 330; Kempf 1960:390; Kempf 1961: 491; Kempf 1972:116; Deyrup, et. al. 1989:93; Lattke 1990:8.

Diagnosis.—Promesonotal suture weakly impressed; node dorsum with transverse costulae and subquadrate costulae and subquadrate subpetiolar process; first gastric sternum with transverse costulae; metacoxal tooth long and thin. Piceous body.

Ecology.—Millipede feeder found in humid forests. The USA record (Deyrup, et. al. 1989:93) is undoubtedly a recent introduction and they have apparently found prey in the local species of millipedes, as they are well established.

Comments.—The number of transverse costulae on the petiolar dorsum can vary from 8 to 14, and those on the pronotum from 13 to 23. Specimens from Argentina tend to have a higher count but there is no gap separating the values. The length of the coxal teeth is variable and bears no relation to the number of petiolar costulae. Propodeal teeth also show variation from a low mound to the usual low, sharp

teeth. Occasional specimens can have up to 4 transverse costulae on the anterior pronotal face, and rarely longitudinal costulae on the petiolar node. Other traits used by Santschi to separate *aculeaticoxae*, such as degree of impression of the promesonotal suture, gastric constriction and gauge of hairs, length vs. width of petiolar node and the mandibular costulation all show continuous variation that is best described as infraspecific.

Specimens Examined.—ARGENTINA, Tucumán: vic. Horco Molle, 750–900m; Tafecillo; La Cavera; 48 km S Jujuy. BOLIVIA, Huachi: Río Beni. BRAZIL, Espiritu Santo: 4 km W Santa Tereza, Res. Nova Lombardia, 900m; Paraná: Foz do Iguaçu; São Paulo: Agudos. COLOMBIA, Magdalena: 3 km SE Minca, 11°08' 74°06'W, 1050m; Pq. Tayrona, Pueblito, 360m. COSTA RICA, Heredia: La Selva; Península de Osa, Pq. Nac. Corcovado, 8°28'N 83°35'W, 0–100m. ECUADOR, Pichincha: 47 km S Santo Domingo, Río Palenque, 215m. GUIANA, Kamakusa. PANAMA, Barro Colorado. PERU, Tingo María: Yurac, 108 km E Tingo María; Puerto Maldonado, 260 m; Panguana, 9°37'S 74°56'W, 220m. USA, Florida: S. Miami. VENEZUELA, Amazonas: Alto Río Mavaca, 2°01'N 65°07'W, 200m.

***Gnamptogenys volcano* Lattke,**
new species
(Fig. 64, 65)

Type Material.—Holotype worker. COSTA RICA, Heredia: 18 km N Volcán Barba, 10°17'N 84°05'W, 800m, 4/14-VII-1986, J. Longino no. 1383–5. Wet forest litter sample. Deposited in LACM. One antenna lacking.

Worker.—Holotype measurements: HL 1.38; ML 0.55; HW 1.18; ED 0.25; SL 1.18; WL 1.93 mm; CI 0.86; SI 1.00; OI 0.21.

Head in frontal view elongate, vertexal margin concave; eyes prominent and situated at mid-length; clypeal lamella relatively long, laterally rounded and medianly concave; mandibles smooth and shining, with prominent piligerous fossae; subtrian-

gular basal angle preceded by a tooth and concavity (or notch); scape when laid back barely surpasses vertexal margin; mesosomal dorsum with longitudinal costulae and propodeal declivity with transverse costulae, in dorsal view the costulae arch posterad and become longitudinal; gaster with longitudinal costulae, including postpetiolar sternum, weakly effaced anteromedianly; metacoxae with dorsobasal tooth, dorsally with transverse costulae and laterally mostly smooth and shining; subpetiolar process with no posterior heel; tibiae and femora smooth and shining. Body with numerous standing golden hairs; body brown, legs and antennae reddish brown.

Queen, Male.—Unknown.

Discussion.—*Gnamptogenys volcano* is close to *sulcata* but the latter can be recognized by the longitudinal costulae on the propodeal declivity, broader head, rounded mandibular basal angle with no tooth and the straight clypeal lamella with acutely angulate sides. The structure of the clypeal lamella, mesepisternum, and mandible make this a striking species within the *sulcata* group.

Etymology.—The name of the species comes from the latin word for volcano, as the type locality is near the Barbas volcano.

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Latitudinal Gradients in North American Braconid Wasp Species Richness and Biology

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Abstract.—Latitudinal trends in the numbers of species and genera of all subfamilies of Braconidae in America north of Mexico were examined by compiling lists of published records for states (USA) and provinces (Canada) and grouping these into approximate latitudinal belts. The data obtained agree well with past studies on the species richness of Ichneumonidae in North America (Janzen 1981) with peaks in numbers of taxa occurring in the belt lying approximately between 37° and 42° North. The ratio of idiobiont to koinobiont genera and species increased monotonically with decreasing latitude.

Most insect groups increase in species richness with decreasing latitude (see Stephens 1989). However, there is a body of evidence that the species richness and diversity of some groups of insect parasitoids, whilst increasing towards the tropics, does so at a lesser rate than does the species richness and diversity of herbivorous insects (Owen & Owen 1974; Gauld 1986; Noyes 1989). Whilst there is good evidence that the species richness and perhaps also diversity of some groups of parasitic Hymenoptera, such as the Chalcidoidea, increases towards the tropics (e.g. Hespeneide 1979), for others it has been suggested that species richness may even be greater in temperate than in tropical regions, a trend referred to as anomalous diversity (Owen & Owen 1974; Janzen & Pond 1975; Janzen et al. 1976). However, these conclusions have been challenged on the grounds of sampling methodology (Morrison et al. 1978; Hespeneide 1979), and also because they mostly deal with just one family, the Ichneumonidae, and the generality of these findings has yet to be demonstrated.

Janzen (1981) examined the latitudinal distributions of members of eight subfamilies of Ichneumonidae in North America

using the catalogues of Townes. These catalogues were based on an enormous amount of work and were therefore taken to be relatively geographically unbiased, though the possibility does exist that since Townes himself did much of his collecting around Michigan, the taxonomic coverage of that part of the United States may have been relatively more complete. However, Janzen's approach does overcome some of the difficulties encountered when working on tropical versus temperate comparisons in that sampling and taxonomic effort within the temperate region has been comparatively evenly distributed and more thorough because of the long history of collecting and revisionary work that has been carried out there. Surprisingly, Janzen found that the peak in North American ichneumonid species richness occurs between 38° and 42° North, i.e. species richness was not found to increase consistently with decreasing latitude. The question remained, however, whether this result was more generally applicable to other groups of parasitic Hymenoptera. Indeed there is a growing body of evidence to suggest that different groups of parasitoids show quite different trends in their species richness with respect to latitude (Gauld 1986; Askew 1990).

The present work attempts to carry out for the Braconidae, a similar exercise to Janzen's (1981) ichneumonid study. The Braconidae are generally accepted as being the extant sister group of the Ichneumonidae (Sharkey & Wahl 1992), and collectively, the two families constitute the superfamily Ichneumonoidea. Juillet (1964) obtained data from samples of ichneumonoids caught in a rotary trap at a single site in Canada, which suggested that members of the Ichneumonidae 'prefer', and hence are more diverse in, cooler and more humid habitats than members of the Braconidae. Thus, it might be expected that braconids will, as a whole, be more species rich at lower latitudes than ichneumonids, and therefore might not show the same peak in species richness that Janzen found for Nearctic Ichneumonidae. Thus, as pointed out by Wharton (1993a), the distribution of species richness in the Braconidae ought to make an interesting comparison with the Ichneumonidae.

Catalogues and descriptions of Nearctic Braconidae usually provide data on the state or province from which material has been recorded or described. We therefore divided the states of the USA and the Canadian provinces collectively into 5 groups such that each group occupied a reasonably constant latitudinal zone with minimal latitudinal overlap between groups (Fig. 1). The areas of the five zones are given in Table 2. Whilst it was not possible to completely avoid overlap, the effect of such overlaps will be to reduce rather than enhance the likelihood of detecting latitudinal gradients, and consequently our results will be conservative. The resolution of latitudinal trends in the present study is necessarily somewhat coarser than that obtained by Janzen (1981) as information on distributions is only readily available in the form of state or province records.

The primary sources of distributional data were the catalogues of Shenefelt

(1969, 1970a, b, 1972, 1973a, b, 1974, 1975, 1978), Shenefelt & Marsh (1976) and Marsh (1979). We then attempted to take into account many of the subsequently published taxonomic changes so as to allow for new synonymies, new generic placements, newly described taxa and new distribution records (van Achterberg 1977, 1979, 1983, 1985, 1986, 1987, 1988a, b; Čapek & Achterberg 1992; Deyrup 1981; Haeselbarth & Loan 1985; Huddleston 1976; Johnson 1987; Loan 1979; Loan & Holliday 1979; Marsh 1988, 1989, 1991, 1993; Mason 1975, 1976a, b, 1978, 1979, 1981, 1987, 1991; Quicke & Kruft 1995; Quicke & Sharkey 1985; Riegel 1987; Rieske et al. 1989; Saffer 1982; Sharkey 1985, 1988; Sharkey & Mason 1986; Sharkey & Wharton 1985, 1994; Shaw 1983, 1985, 1992, 1993; Stry & Marsh 1982; Wharton 1977a, b, 1980, 1983, 1986, 1988, 1993b, 1994; Wharton & Quicke 1988; Wharton et al. 1989; Wheeler & Loan 1984; Whitfield 1985, 1988a, b; Whitfield & van Achterberg 1987; Whitfield & Mason 1994; Williams 1985, 1988). In addition, a few unpublished data were included for the following taxa: *Vipio* (Braconinae) (Inayatullah 1992); *Pholetesor* (Microgastrinae) (J. Whitfield, in press); undescribed genus of Euphorinae (S. R. Shaw, pers. comm.). The genus *Celerion* is excluded as its subfamilial status is questionable (Marsh, pers. comm.). No data are included for introduced species.

The treatment of subfamilies largely follows that of Quicke & Achterberg (1990) except that the Hormiini and Meteorini are treated here as separate subfamilies.

No pretence is made that this taxonomic treatment is complete, but it is hoped that it is unbiased and, therefore, that any errors that may have been included and any omissions there may be will not affect the results substantially.

RESULTS AND DISCUSSION

The numbers of genera and species of each subfamily recorded as occurring in

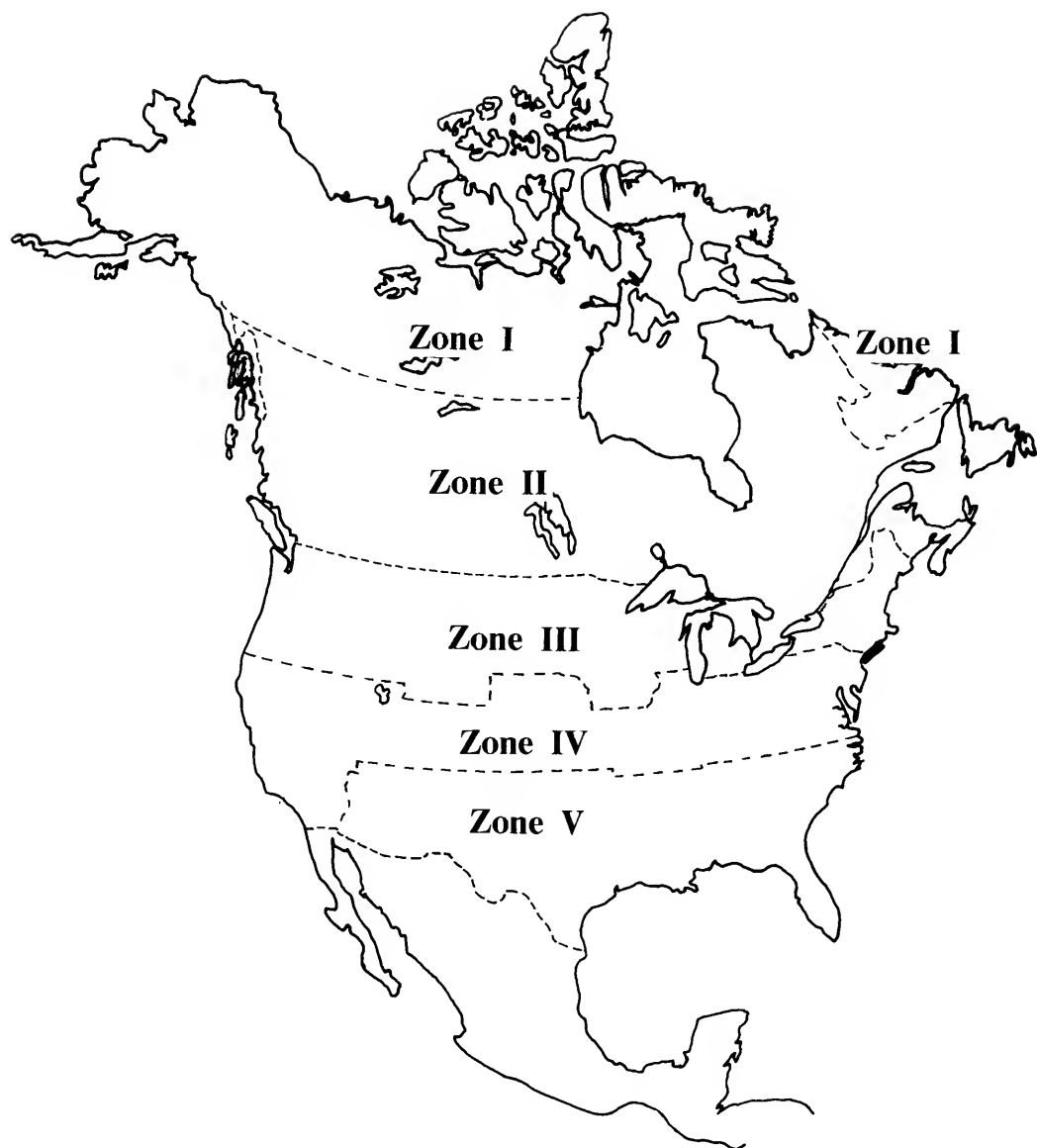


Fig. 1. Map of North America showing boudaries of latitudinal zones employed in the present study.

each of the five latitudinal zones are presented in Tables 1 and 2. The subfamilies are arranged in two groups, the first being idiobionts (Table 1) and the second koinobionts (Table 2). As expected, different subfamilies showed markedly different latitudinal trends, though nearly all showed maximum generic and specific representation in our latitudinal zone IV

which corresponds approximately to the latitudinal range from 37° and 42° North. None of the larger subfamilies was found to be most speciose in zone V. Four of these, the Braconinae, Microgastrinae, Macrocentrinae and Opiinae were most diverse in zone III. Our data for the Alysiinae, usually considered a more temperate and northern group, suggest that within

Table 1. Distributions of genera and species of braconid subfamilies with respect to latitudinal zones (see Fig. 1). Idiobiont taxa

| | Subfamilies | | | | | | Total |
|----------|-------------|---------------------|------------|------------|-------------|-----------|-------|
| | Rhyssalinae | Histero- merinae | Doryctinae | Braconinae | Exothecinae | Hormiinae | |
| Genera | | | | | | | |
| Zone I | 0 | 0 | 2 | 3 | 2 | 1 | 8 |
| Zone II | 2 | 1 | 8 | 9 | 3 | 2 | 25 |
| Zone III | 1 | 1 | 16 | 8 | 4 | 4 | 34 |
| Zone IV | 2 | 1 | 20 | 7 | 3 | 6 | 39 |
| Zone V | 1 | 1 | 28 | 10 | 2 | 8 | 50 |
| Species | | | | | | | |
| Zone I | 0 | 0 | 2 | 4 | 3 | 1 | 10 |
| Zone II | 2 | 1 | 35 | 67 | 4 | 3 | 112 |
| Zone III | 5 | 1 | 72 | 108 | 5 | 5 | 196 |
| Zone IV | 4 | 1 | 111 | 104 | 3 | 12 | 235 |
| Zone V | 1 | 1 | 105 | 86 | 2 | 11 | 206 |

North America, it is at its richest in the middle latitudes of the U.S.A. (zone IV) as with most other subfamilies.

Table 3 provides a comparison of the relative latitudinal distributions of braconid genera and species according to zone and in terms of taxa per unit area. Additionally, it shows the total numbers of idiobiont and koinobiont taxa and the ratios of numbers of koinobiont to idiobiont taxa in each latitudinal zone. The latter show consistent trends for both genera and species, with the ratio of koinobionts to idiobionts decreasing with decreasing latitude.

It has long been recognised that some subfamilies of Braconidae are most species rich in the temperate region whilst others are tropicocentric. For example, the Alysiinae, which are entirely koinobiont endoparasitoids of Diptera, are a principally northern group, and whilst there are many undescribed tropical members of the genus *Asobara*, a group that attacks *Drosophilidae*, more detailed knowledge of these is not likely to change our concept of the subfamilies overall distribution to a major degree. In contrast, the Agathidinae and Cardiochilinae, two groups of koinobiont endoparasitoids of *Lepidoptera* larvae, are both most speciose in the tropical region

(Sharkey 1992; Huddleston & Walker 1988), and the latter in particular is rather species poor in temperate latitudes. Some groups are restricted in latitudinal range by the distributions of their hosts. For example, members of the ichneumonid subfamily Ctenopelmatinae, most tryphonine ichneumonids, and the braconid tribes Ichneutini and Proteropini (both usually treated as belonging to the Ichneutinae; see Sharkey & Wharton 1994) are all endoparasitoids of sawflies, and since sawflies are most abundant in temperate regions they are likely to support a higher species richness of parasitoids there.

In the case of the Braconidae, life history strategy, idiobioncy and koinobioncy (Askew & Shaw 1986), is very tightly linked with whether the wasps develop as ecto- or endoparasites respectively (Quicke & Achterberg 1990; Shaw & Huddleston 1991). It is not possible therefore, to discern which of these life history features is most responsible for the observed trends. Further, as biology is usually consistent within subfamilies within the Braconidae (Shaw & Huddleston 1991), any latitudinal trends in the ratios of idiobiont to koinobiont taxa will necessarily involve the differential occurrence or representation of subfamilies.

Table 2. Distributions of genera and species of braconid subfamilies with respect to latitudinal zones (see Fig. 1). Koinobiont subfamilies

| | Subfamilies | | | | | | | | | | | |
|----------|-------------|-----------------|--------|----------|-----------|-------------|-------------|-----------|------------|---------------|-----------|----------------|
| | Rogadinae | Gnamptodontinae | Opinae | Alysinae | Aphidinae | Ichneutinae | Dirrhopinae | Adeliinae | Cheloninae | Mendesellinae | Miracinae | Cardiochilinae |
| Genera | | | | | | | | | | | | |
| Zone I | 2 | 1 | 2 | 13 | 6 | 1 | 0 | 0 | 3 | 0 | 0 | 0 |
| Zone II | 4 | 1 | 6 | 26 | 16 | 3 | 0 | 0 | 5 | 0 | 1 | 1 |
| Zone III | 7 | 1 | 7 | 28 | 13 | 3 | 1 | 2 | 5 | 0 | 1 | 1 |
| Zone IV | 7 | 1 | 6 | 30 | 12 | 4 | 1 | 2 | 5 | 0 | 1 | 1 |
| Zone V | 7 | 2 | 7 | 18 | 13 | 5 | 1 | 2 | 5 | 1 | 1 | 1 |
| Species | | | | | | | | | | | | |
| Zone I | 3 | 2 | 14 | 73 | 10 | 3 | 0 | 0 | 10 | 0 | 0 | 0 |
| Zone II | 14 | 1 | 64 | 77 | 57 | 4 | 0 | 0 | 55 | 0 | 3 | 3 |
| Zone III | 33 | 2 | 147 | 131 | 54 | 6 | 1 | 2 | 77 | 0 | 4 | 10 |
| Zone IV | 36 | 4 | 111 | 158 | 70 | 6 | 1 | 4 | 98 | 0 | 5 | 26 |
| Zone V | 31 | 5 | 122 | 55 | 34 | 7 | 1 | 2 | 50 | 1 | 5 | 24 |

Whilst straightforward taxonomic effects are undoubtedly involved in determining the distributions of some groups, there is a growing evidence that trends in species richness and diversity may be correlated with life history strategy. In particular, idiobionts whose hosts by definition do not develop further following initial parasitization (Askew & Shaw 1986) appear to be more species rich at lower latitudes than parasitoid taxa that display the opposite strategy, the koinobionts.

Hawkins et al. (1992) in an attempt to understand better the latitudinal trends in parasitoid diversity in North America, took a different approach in that they concentrated on parasitoid assemblage size per host rather than on the numbers of species in random field samples. Their data showed that latitudinal trends in species richness are influenced not only by whether the parasitoids display idiobiont or koinobiont life history strategies but also by host feeding niche. In particular, they found that the diversity of parasitoids of exophytic hosts decreased with decreasing latitude but that the diversity of

those attacking endophytic hosts increased.

Several hypotheses have been proposed to account for declines in the species richness of some parasitoid groups with decreasing latitude and for trends in the ratios of idiobionts to koinobionts. These include Gauld et al.'s (1992) "nasty" host hypothesis, resource fragmentation hypotheses (Janzen & Pond 1975; Janzen 1981), interphyletic competition (Eggleton & Gaston 1990), parasitoid predation effects (Gauld 1987), host predation effects (Rathcke & Price 1976), and limited speciation opportunity as a result of supposed low host recruitment potential (Shaw 1994). These are not dealt with in detail here as they are reviewed in detail by Hawkins (1994).

Our data show that overall, the latitudinal variation in species richness in North American Braconidae closely resembles that found by Janzen (1981) for Ichneumonidae, with a peak near the central latitudes of the USA and with a distinct decline in the numbers of species and genera occurring in the southernmost

Table 2. Extended

| Subfamilies | | | | | | | | | | | | | | | |
|-----------------|------------|------------|-------------|-------------|-----------|---------------|--------------|-------------|--------------|----------------|------------|----------|---------------|-------------|-------|
| Microgasterinae | Euphorinae | Meteorinae | Neoneurinae | Agathidinae | Orgilinae | Microtyphinae | Cenocoelinae | Homolobinae | Charmontinae | Macrocentrinae | Helconinae | Blacinae | Meteorideinae | Sigalphinae | Total |
| 11 | 6 | 2 | 0 | 2 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 2 | 0 | 0 | 58 |
| 22 | 14 | 2 | 2 | 6 | 1 | 1 | 1 | 2 | 1 | 2 | 12 | 2 | 0 | 1 | 131 |
| 23 | 17 | 2 | 2 | 5 | 1 | 1 | 1 | 2 | 1 | 2 | 13 | 2 | 1 | 1 | 143 |
| 21 | 16 | 2 | 2 | 7 | 2 | 1 | 1 | 1 | 1 | 2 | 15 | 1 | 0 | 1 | 143 |
| 10 | 15 | 2 | 2 | 8 | 2 | 1 | 1 | 2 | 1 | 2 | 10 | 2 | 1 | 1 | 123 |
| 18 | 6 | 7 | 0 | 2 | 7 | 1 | 0 | 1 | 2 | 2 | 2 | 6 | 0 | 0 | 171 |
| 122 | 61 | 25 | 3 | 25 | 31 | 1 | 4 | 4 | 2 | 25 | 25 | 17 | 0 | 1 | 634 |
| 182 | 41 | 30 | 9 | 53 | 49 | 1 | 5 | 4 | 1 | 36 | 57 | 14 | 1 | 1 | 961 |
| 169 | 43 | 32 | 8 | 61 | 55 | 1 | 8 | 3 | 2 | 32 | 70 | 13 | 0 | 1 | 1025 |
| 125 | 33 | 24 | 5 | 51 | 34 | 1 | 8 | 6 | 2 | 23 | 58 | 11 | 1 | 1 | 725 |

states. We have no evidence that sampling in the southern states has been significantly less intense than in more northerly ones though the possibility cannot be excluded. Further, it should be noted that in all five zones some states and provinces have been collected in much more intensively than others. California, a state that has been extensively collected, was in-

cluded in our Zone IV, though it could equally justifiably have been included in Zone V as it straddles the boundary latitude more or less evenly. Reanalysis of the data set with California transferred to Zone V does not reduce the peaks in species and generic richness in zone IV to any great extent.

Extrapolation of the observed trend in

Table 3. Summary of latitudinal distributions of genera and species of Braconidae in North America and ratios of koinobiont to idiobiont taxa

| | Total no. of taxa | Area (10 ⁶ km ²) | Total taxa per 10 ⁶ km ² | No. of idiobiont taxa | No. of koinobiont taxa | Koinobiont/Idiobiont |
|----------|-------------------|---|--|-----------------------|------------------------|----------------------|
| Genera | | | | | | |
| Zone I | 66 | 5.19 | 12.3 | 8 | 58 | 7.25 |
| Zone II | 156 | 5.76 | 26.9 | 25 | 131 | 5.20 |
| Zone III | 177 | 2.62 | 66.9 | 34 | 143 | 4.17 |
| Zone IV | 182 | 2.57 | 70.0 | 39 | 143 | 3.64 |
| Zone V | 172 | 2.63 | 63.8 | 50 | 122 | 2.42 |
| Species | | | | | | |
| Zone I | 181 | 5.19 | 34.1 | 10 | 171 | 17.10 |
| Zone II | 746 | 5.76 | 127.4 | 112 | 634 | 5.66 |
| Zone III | 1157 | 2.62 | 437.4 | 196 | 961 | 4.90 |
| Zone IV | 1260 | 2.57 | 486.8 | 235 | 1025 | 4.36 |
| Zone V | 930 | 2.63 | 351.3 | 206 | 724 | 3.51 |

species richness in North America to more general, temperate/tropical species richness and diversity questions would be unwise. One reason for caution in this respect is that a substantial part of the southern U.S.A. and northern Mexico is markedly arid, and this may restrict parasitoid species richness as it appears to do in North Africa (unpubl. data). Further, even in areas of higher annual rainfall, ichneumonoids may still be limited by water availability since it has been proposed that many may need to drink on a daily basis and rains are typically less regular (Townes 1971). Townes suggested that dew formation may be equally if not more important than rainfall per se in regulating numbers and species richness of ichneumonoids in warmer climates, and that it is for this reason that altitude is an important factor in determining ichneumonoid species richness in the tropics, dew forming more regularly with increasing altitude. In the case of the Southern U.S.A., much of the less arid south is at low altitude and therefore may experience dew less regularly than required by many species of parasitoids. However, interpretation of dew and rainfall data is likely to be far from a simple matter of examining the mean annual number of dew days for particular states, and if water availability is an important factor in limiting ichneumonoid species richness in the more southern states, then rainfall, season, temperature and dew frequency are likely to be involved together in a complex interaction. Further, other important sources of water for many insects of arid region are nectar and honeydew, and availability of these, and their utilization by ichneumonoids, may also need to be considered.

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Revision of the World Genera of the Subtribe Stigmina (Hymenoptera: Apoidea: Sphecidae: Pemphredoninae), Part 1

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Abstract.—The following new genera are described: *Araucastigmus*, *Aykhustigmus*, *Incastigmus*, *Llaqhastigmus*, and *Tzustigmus*. The following new species are described: *Araucastigmus masneri*, *yanillus*; *Aykhustigmus fritzi*, *patanawi*, *phasti*, *warawa*; *Incastigmus inti*; *Llaqhastigmus ambiguus*, *australis*, *chutiyana*, *colombianus*, *ecuatorialis*, *jatunkirus*, *llutaniis*, *mantanti*, *muthus*, *nigricollaris*, *santan-deranus*, *sapanis*, *shachus*, *sharkeyi*; *Parastigmus huecuvus*, *nina*; *Tzustigmus khmer*, *syam*, *veda*, and *wuming*. New synonymy: *Stigmus smithii* Ashmead is placed under *Incastigmus thoracicus* (Ashmead). A key to world genera is presented, and history, biology, generic relationships, and biogeography are discussed. Species of *Araucastigmus*, *Aykhustigmus*, *Llaqhastigmus* and *Parastigmus* are keyed and described, and their distributions are presented.

INTRODUCTION

This contribution is intended as the first in a series of papers dealing with the world species of the Stigmina. Members of the Stigmina are small, generally 3 to 5mm in length, and black or red and black in coloration. The group contains an estimated 150 species distributed in all areas except the polar regions but for the most part is found throughout the southern hemisphere tropics. This first paper describes five new genera, *Tzustigmus*, *Araucastigmus*, *Aykhustigmus*, *Incastigmus* and *Llaqhastigmus*, treats the species of the smaller genera, reviews biology, taxonomic history, and presents an analysis of generic phylogeny before considering the biogeography of the Stigmina. Future papers will deal with the species of *Incastigmus*, *Stigmus*, and *Carinostigmus*.

Morphological Terms And Symbols.—Terminology generally follows Bohart and Menke (1976) but in some cases terms need clarification and some new terms are introduced. They are listed below:

Appressed setae: setae forming an angle close to 0° with the body surface.

Carinate: a series of relatively large ridges (see microcarinate below) that do not impart a dull appearance to the body.

Lateral sphere of propodeum: area of propodeum curving between propodeal enclosure and side.

LOD: maximum diameter of lateral ocellus.

Mesosoma: the thorax plus the propodeum.

Metasoma: the apparent abdomen consisting of the abdomen excluding the first segment or propodeum.

Micropore field (Fig. 32): a grouping of very small pores usually visible only by scanning electron microscope, but by stereomicroscope apparent as a discrete microsculpture patch.

Microcarinate: a series of parallel ridges so fine as to impart a dull appearance to the body.

Microsculpture: minute sculpture imparting a dull appearance to the body.

OOD: least distance between lateral ocellus and eye.

Preomaular area: = preomaular area of Bohart and Menke (1976).

Sternum: metasomal sternum.

Tergum: metasomal tergum.

Transscutellar sulcus: the anterior transverse sulcus of the scutellum, immediately posterior to the transscutal articulation.

Transverse sulcus: on pronotal dorsum, the transverse sulcus immediately posterior to the transverse carina.

*: holotype examined.

Species Treatments.—Descriptions of all included species are provided. Descriptions of new species are based on all the material examined. In species demonstrating variability descriptions are based on representatives of the most prevalent phenotype with variation noted throughout the description. Collection data for the primary type material are presented exactly as they appear on the label, thus several spellings for the same locality and collector, and several formats for date of collection will be encountered. Collection data for secondary type specimens are presented in a standardized format organized by country and state or province. In previously described species the Material Examined section lists only localities of collection.

Sources Of Material.—Over 10,000 specimens from 47 institutions were amassed for this study. The following institutions have provided material used in this paper or loaned types. The abbreviation preceding the institution is that used in the text to designate type repositories.

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|-------------|---|--------------|---|
| AEI | American Entomological Institute, 3005 sw 56th Ave. Gainesville, FLORIDA 32608 USA. V.K. Gupta, the late H.K. Townes, D. Wahl. | BMNH | The Natural History Museum, Cromwell Road, London, SW7 5BD ENGLAND. C.R. Vardy. |
| ANIC | Australian National Insect Collection, CSIRO, Division of Entomology, GPO Box 1700 Canberra, ACT 2601, AUSTRALIA. I.D. Naumann. | BRD | Biosystematics Research Division, CLBRR, Agriculture Canada, Research Branch, K.W. Neatby Building, Ottawa, Ontario, CANADA K1A 0C6. L. Masner. |
| BISH | Bishop Museum, 1525 Bernice Street, P.O. Box 19000-A Honolulu, HAWAII 96819 USA. G.M. Nishida. | CARN | Carnegie Museum, 4400 Forbes Avenue, Pittsburgh, PENNSYLVANIA 15213 USA. J.E. Rawlings. |
| | | CAS | California Academy of Sciences, Golden Gate Park, San Francisco, CALIFORNIA 94118 USA. W.J. Pulawski. |
| | | FSCA | Florida State Collection of Arthropods, Division of Plant Industry, Department of Agriculture, Gainesville, FLORIDA 32601 USA. L.A. Stange. |
| | | IIES | Consejo Nacional de Investigaciones Cientificas y Tecnicas, Instituto de Investigaciones Entomologicas Salta (INESALT), 9 de Julio 14-Casilla de Correo 3, 4405 Rosario de Lerma, Salta, ARGENTINA. M.A. Fritz. |
| | | LILLO | Fundacion Miguel Lillo, Instituto de Zoologia Miguel Lillo 251, 4000 San Miguel de Tucuman, ARGENTINA. A. Willink. |
| | | MACN | Museo Argentino de Ciencias Naturales, Seccion Entomologia, Angel Gallardo 470, Casilla de Correo 220, Sucursal 5, 1405 Buenos Aires, ARGENTINA. A. Roig Alsina. |
| | | MCSN | Museo Civico Di Storia Naturale "Giacomo Doria" I-16121 Genova, via Brigata Liguria, N. 9, ITALY. V. Raineri. |
| | | MCZ | Museum of Comparative Zoology, The Agassiz Museum, Harvard University, Cambridge, MASSACHUSETTS 02138 USA. C. Vogt. |
| | | MPEG | Museu Paraense Emilio Goeldi, Av. Magalhaes Barata, 376—C.P. |

399, CEP 66000-Belem, Para,
BRASIL. W.L. Overal.

HISTORY

NMW Naturhistorisches Museum Wien,
2. Zoologische Abteilung (Insek-
ten), A-1014 Wien, Burgring 7,
ÖSTERREICH (Austria). M. Fi-
scher.

OSU Oregon State University, Depart-
ment of Entomology, Corvallis,
OREGON 97331 USA. G.R. Fer-
guson.

PMA Provincial Museum of Alberta,
12845-102 Avenue, Edmonton,
Alberta, CANADA T5N 0M6.

RNH Rijksmuseum van Natuurlijke
Historie, Raamsteeg 2, Leiden,
NETHERLANDS. K. van Ach-
terberg.

SEM Snow Entomological Museum,
University of Kansas, Lawrence,
KANSAS 66045 USA. R.W.
Brooks.

TMA Természettudományi Múzeum
Allattara, H-1088 Budapest, Bar-
oss u. 13 HUNGARY. J. Papp.

UCV Instituto de Zoología Agrícola,
Universidad Central de Vene-
zuela, Maracay 2101-A, VENE-
ZUELA. J. Luis García.

USNM Systematic Entomology Labora-
tory, USDA % U.S. National
Museum, NHB 168, Washing-
ton, D.C. 20560 U.S.A. A.S. Men-
ke.

ZIN Insect Systematics Laboratory,
Zoological Institute, Russian
Academy of Sciences, Sankt-Pe-
terburg 199034 RUSSIAN FED-
ERATION.

ZMD Zoologisk Museum, Department
of Entomology, Universitetspar-
ken 15, DK 2100 Kobenhavn,
DANMARK (Denmark). O.
Lomholdt.

ZMMU Zoological Museum of the Mos-
cow State University, Herzen
Street 6, Moscow 103009 RUS-
SIAN FEDERATION. A.V. An-
tropov.

G.W.F. Panzer (1804) described the ge-
nus *Stigmus* for a single species, *Stigmus*
pendulus from Europe. Species description
in the Stigmina accumulated more or less
ad hoc until Kohl (1890) produced the first
world synthesis of *Stigmus* and related
genera. His revision of the *Pemphredon* ge-
nus group provided a sound generic
grouping that is still, a century later, the
basis of modern classification. Over the
period of 1890–1911, 24 species were de-
scribed by such notable authorities as
Kohl (1892, 1905), Cameron (1891), Fox
(1892, 1897), Ashmead (1900), Mantero
(1901), Rohwer (1911) and Strand (1911).
During this period Turner (1907) de-
scribed the genus *Paracrabro* from Austr-
lia.

By 1920 most of the descriptive work
had shifted to fauna of the southern hemi-
sphere culminating with Tsuneki's (1954)
description of a new subgenus, *Carinostig-
mus*, accompanying a revision of the Asian
and European *Stigmus*. In subsequent pa-
pers Tsuneki (1963, 1966, 1971) went on to
describe numerous species and subspecies
in the Oriental Region while Leclercq
(1959) described species from the Afro-
tropical Region. The Nearctic fauna was
revised by Krombein (1973) at which time
he described a new subgenus *Atopostig-
mus*. Work on all groups of sphecoid
wasps reached a high point when Bohart
and Menke (1976) published a world ge-
neric revision, a landmark synthesis un-
precedented in the history of the group.
That work delineated the subtribe Stig-
mina to which the following 7 genera
were assigned: *Arpactophilus*, *Paracrabro*,
Stigmus, *Carinostigmus*, *Spilomena*, *Micro-
stigmus*, and *Xysma*. Subsequently Krom-
bein (1984) described 4 new species of *Car-
inostigmus* and a new subgenus *Perissostig-
mus* from Sri Lanka. Budrys (1987) de-
scribed new species from the former
Soviet far east. Antropov (1992) described

the genus *Parastigmus* from the Neotropical Region.

Among the most important publications influencing the classification of the Stigmina was Menke's (1989) paper on new species of *Arpactophilus* from New Guinea. The author indicated that the subtribal limits proposed by Bohart and Menke in the 1976 world revision should be reconsidered. He established a new subtribe, *Spilomenina*, containing *Arpactophilus*, *Spilomena*, *Microstigmus* and *Xysma*. Furthermore Menke was able to unite these genera using a newly discovered apotypic character state, that of reduced papal segmentation. Menke's work first of all reduced the Stigmina to 3 genera: *Paracrabro* (1 Australian species), *Stigmus* (30 species, Holarctic, Neotropical and Oriental), and *Carinostigmus* (25 species, Afrotropical and Oriental). Secondly, no synapotypic character states supporting the 3 genera remaining in the Stigmina were known, which meant that the Stigmina could be a plesiotypic assemblage representing an artificial rather than a natural grouping. This paper provides ample evidence of the monophyly of the Stigmina and indicates that 9 genera and about 150 species are included.

BIOLOGY

Published records (Arnold 1924; Eickworth 1967; Iwata 1964; Janvier 1962; Krombein 1956, 1958a, 1958b, 1961, 1963, 1984; Rau 1928; Richardson 1915; Smith 1923; Tsuneki 1970; Wasbauer and Simonds 1964; Yasumatsu and Watanabe 1964) indicate that *Stigmus* and *Carinostigmus* nest in twigs or pre-existing cavities and prey on aphids (Homoptera: Aphidoidea). Twig nests are usually constructed by excavating pithy twigs like *Rubrus*, *Sambucus*, or *Sassafras* among others. Pre-existing cavities include straws of thatch, holes or borings in timber and galls. Nests vary in length from 8cm to half a metre, the cells are constructed in linear series separated by masticated wood or plugs of

pith. Cells are mass provisioned or possibly progressively provisioned with 12–30 aphids depending on prey size and species of wasp. Progressive provisioning creates a subsocial situation where mothers and daughters are present in the same nest. Iwata (1964) observed progressive provisioning in nests of *Carinostigmus iwatai* (Tsuneki) and found larvae and adults of different ages in nests of *C. monstrosus* (Tsuneki). The only reported cleptoparasites are chrysidid wasps of the genus *Omalus*.

Unpublished or anecdotal records indicate some species of Stigmina are sand nesting, a presumed plesiotypic character state. Krombein (1973, 1984) in his revisions of Nearctic *Stigmus* and Sri Lankan *Carinostigmus*, lent some credibility to these observations when he noted nesting differences in females with 2 or 3 mandibular teeth. Females with 3 mandibular teeth excavated nests in pithy twigs or stems while those with 2 teeth used pre-existing cavities in the ground. The implication is that those species constructing nests evolve more complex mandibular dentition presumably to perform more specialized tasks. *Microstigmus* (*Spilomenina*) have a bidentate mandible that is not used in construction of a complex nest suspended beneath a leaf and housing multiple generations. The foregoing indicates that mandibular dentition likely bears a straightforward relationship to nest construction when mandibles are employed for that purpose.

More reliable evidence of sand nesting can be inferred from the presence of a fore tarsal rake and a broad pygidial plate in the female or a remnant of that plate in the male. The fore tarsal rake is a series of elongate setae which are used to move sand. Members of Stigmina lack a fore tarsal rake but have spatulate setae on the rake area, possibly a secondary adaptation to manipulation of nest material. The pygidial plate is a flat specialized area defined by a carina or groove on the 6th

metasomal tergum in the female and the 7th in the male. In sand nesting species this plate occupies a much greater proportion of the tergum than in twig or cavity nesting species. Almost all Stigmina have a narrow pygidial plate occupying a small fraction of the tergum indicating twig or cavity nesting behaviour. A few species have an intermediate pygidial plate and several Argentine species have a large pygidial plate with a remnant of this plate in the male. Manfredo Fritz (personal communication) has observed sand nesting *Stigmus* in Argentina, he was unable to capture any specimens. Specimens from his collection, used in this study, contained females with relatively large pygidial plates and with remnants in several males, possibly representing the only true sand nesting Stigmina.

In summary, biological observations, although detailed in several instances, are available for few species only. More observations are necessary to document nest construction and the existence of social behavior in the group. The Stigmina appear to be twig or cavity nesting and restrict prey to aphids. There is some anecdotal evidence of sand nesting behaviour in southern Neotropical species. A number of new genera have no behavioral data whatever. Observations on these genera are often impeded by the small size of the individuals but would offer a fertile field of study to a dedicated biologist.

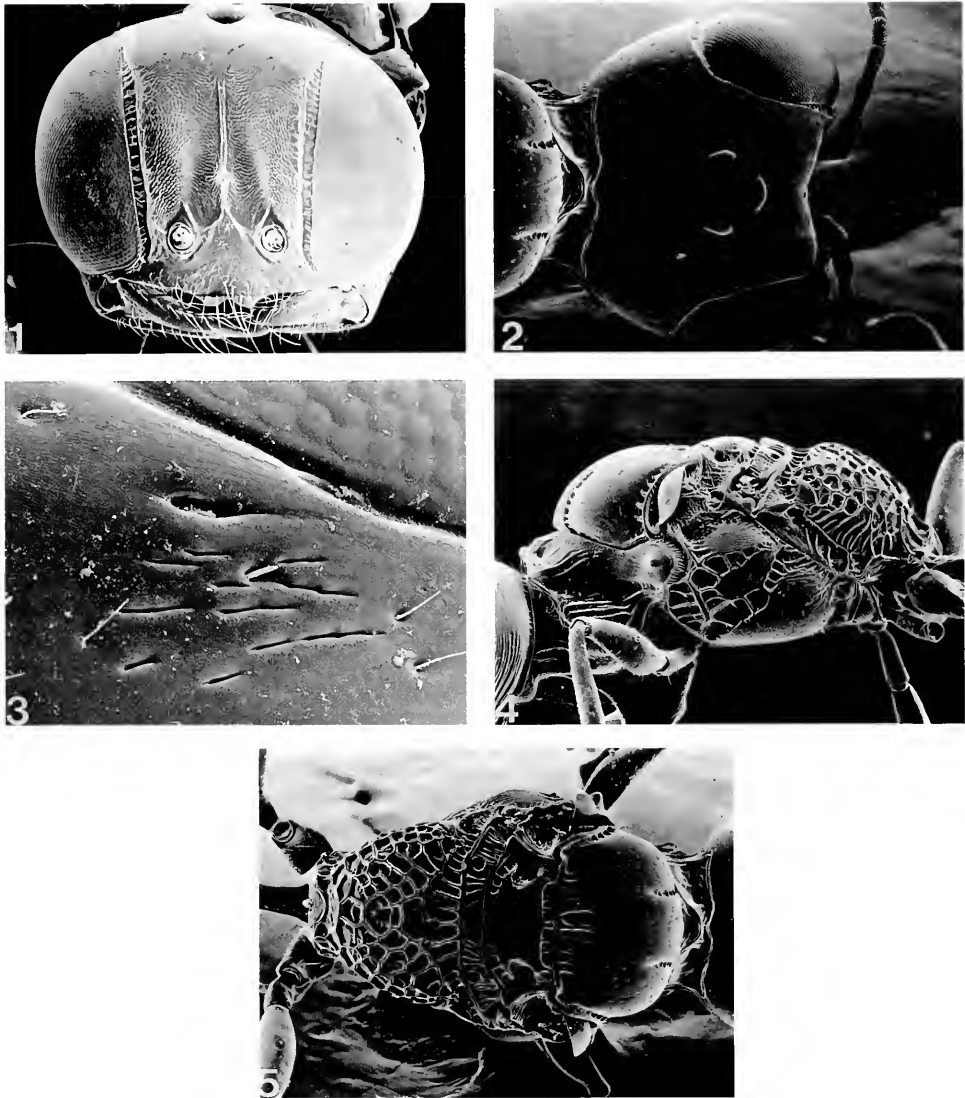
SUBTRIBE STIGMINA

Diagnosis.—The Stigmina, as here defined, includes 9 genera with a microsetal or micropore fields laterally on metasomal sternum II (Figs. 44, 45), more or less centrally on the fore wing stigma (Figs. 46, 47) and on the vertex between the lateral ocellus and the compound eye (Figs. 3, 8, 20, 26, 32). The latter character is not fully developed in several genera but consists of several pits in a small depression. The stigmal pit field is diffuse in 11 species from Chile and Argentina and

may not be readily apparent in these instances. These characters are found in all members of the Stigmina and nowhere else in the Pemphredoninae. They are thus autapotypies that unambiguously delineate the Stigmina. Described genera include *Carinostigmus* Tsuneki, *Paracrabro* Turner, *Parastigmus* Antropov, and *Stigmus* Panzer. In addition to *Paracrabro* and *Parastigmus*, five new genera are proposed and 33 of the 58 species are treated in the present paper: *Tzustigmus* (5 species, Oriental, far eastern Palearctic), *Parastigmus* (4 species, southern Neotropical), *Araucastigmus* (3 species, Chile), *Paracrabro* (1 species, Australian), *Aykhustigmus* (4 species, Neotropical), *Incastigmus* (25 species, Neotropical), and *Llaqhastigmus* (14 species, Neotropical).

Description.—Head. Palpal formula 6–4; mandibular socket closed; antennal sockets placed low on frons near or touching clypeus (Fig. 1); frons unmodified by grooves, except occasionally along inner eye margin; vertex with a micropore field or at least a few associated pits between lateral ocellus and eye (Figs. 3, 8, 20, 26, 32); genal setae usually normal, not elongate setae scattered among short setae (exceptions among some males of *Stigmus* and *Carinostigmus*).

Mesosoma. Pronotum with transverse carina present, at least laterally (Fig. 2); omaulus present; episternal sulcus undeveloped; hypersternaulus present, obliquely oriented across mesopleuron (Fig. 4); fore tarsus of female without rake; mid coxa with oblique dorsal carina; inner hind coxal carina absent; hind coxa without elongate bristle; metasternum with shallow posterior emargination; propodeal enclosure present (Fig. 10); stigma of fore wing enlarged, lenticular with discrete micropore field (Figs. 46, 47); marginal cell normal size, subequal to or larger than stigma, closed and bordering anterior wing margin; 2 submarginal cells; submarginal cell II quadrate; submarginal cell I out of line with respect to marginal



Figs. 1-5. *Carinostigmus* sp. ♀. 1, Head, frontal view. 2, head and prothorax, dorsal view. 3, micropore field between lateral ocellus and compound eye. 4, mesosoma, lateral view. 5, mesosoma, dorsal view.

and discoidal cells; submarginal cell I without spur, closed; recurrent vein received by submarginal cell I; 2 discoidal cells; hind wing cells closed.

Metasoma. Petiole present, longer than wide, setae short, scattered over surface; tergum I without lateral carina; male ster-

na without elongate specialized setae; sterna II and often III with lateral microsetal patches (Figs. 44, 45); sternum VI without apical pegs; pygidial plate present in female, almost always absent in male; sternum VIII of male elongate, volsella divided into digitus and cuspis.

KEY TO GENERA OF STIGMINA

| | |
|---|--|
| 1. Hind wing submedian cell reduced, cu-a positioned about halfway from wing base to origin of media (Fig. 50); Old World, except Australian Region | <i>Carinostigmus</i> Tsuneki |
| 1'. Hind wing submedian cell normal size, cu-a positioned next to origin of media (Fig. 49) | 2 |
| 2. Hind wing media diverging beyond cu-a (Fig. 49) or mesopleuron coarsely areolate to sternopleural region (Figs. 22, 28) | 3 |
| 2'. Hind wing media diverging before cu-a (Fig. 48); mesopleuron not entirely coarsely sculptured (Fig. 34) | 5 |
| 3. Mesopleuron coarsely sculptured to sternopleural region (Figs. 22, 28); male with prominent genal carina separated from mid outer orbit by a distance subequal to basal width of mandible (Fig. 21); Neotropical | <i>Aykhustigmus</i> Finnermore, new genus |
| 3'. Mesopleuron mostly unsculptured, shiny; genal carina, if present, close to eye margin (Fig. 9) | 4 |
| 4. Interantennal tubercle absent (Fig. 40); eyes not margined by a carina; petiole carinate; Japan | <i>Stigmus</i> Panzer, in part |
| 4'. Interantennal tubercle present (Fig. 7); eyes margined by a carina (Fig. 9); petiole smooth, round, at most microcarinate; Oriental, far eastern Palearctic | <i>Tzustigmus</i> Finnermore, new genus |
| 5. Acetabular carina absent (Fig. 11); southern Neotropical | 6 |
| 5'. Acetabular carina present (Fig. 43); widespread | 7 |
| 6. Pygidial plate small, narrow, present in female only; mandible in male bidentate and in female tridentate at apex; body shiny, without microsculpture (Figs. 14, 15); Chile | <i>Araucastigmus</i> Finnermore, new genus |
| 6'. Pygidial plate broad, present in both sexes, evanescent in male; mandible of both sexes bidentate at apex; microsculpture present on head and often most of body; Argentina, Chile | <i>Parastigmus</i> Antropov |
| 7. Vertex micropore field absent; Australia | <i>Paracrabro</i> Turner |
| 7'. Vertex micropore field present (Figs. 20, 26, 32) | 8 |
| 8. Mandibles in male bidentate, female uni-, bi-, or usually tridentate; male clypeal apex usually with lateral bevel (Fig. 42); scutum without trace of median groove or posteromedian pit but may be ridged (Fig. 41); apicoventral mandibular tooth in female, acute (Fig. 39); widespread, except Afrotropical and Australian Regions . . | <i>Stigmus</i> Panzer, in part |
| 8'. Mandibles tridentate in both sexes; male clypeal apex without bevel; scutum usually with median groove or posteromedian pit (Figs. 33, 35); females lacking median scutal groove have apicoventral mandibular tooth enlarged and broadly truncate (Fig. 37); Neotropical | 9 |
| 9. Scutum with median groove or posteromedian pit (Figs. 33, 35); apicoventral mandibular tooth in female, acute (Fig. 39); labrum quadrilobed; throughout Neotropical Region | <i>Incastigmus</i> Finnermore, new genus |
| 9'. Scutum without trace of median groove or posteromedian pit (Fig. 38); female with apicoventral mandibular tooth enlarged, broadly truncate (Fig. 37); labrum usually bilobed, rarely 4-lobed; Neotropical: restricted to continental South America | <i>Llaqhastigmus</i> Finnermore, new genus |

Tzustigmus Fিন্নমোৰ, new genus
(Figs. 6–11, 44, 45, 47)

Derivation of Name.—Tzu, a Chinese term meaning master or teacher, in this case referring to the relatively basal position of the genus within the Stigmina and its subsequent value in the inference of polarization of character states in the subtribe.

Diagnosis.—The combination of an interantennal tubercle, the hind wing media diverging just beyond cu-a, and a mostly unsculptured mesopleuron will separate this genus from all others in the Stigmina.

Description.—Head. Labrum quadri-lobed with median emargination narrow and deep; mandibular apex bidentate in male, tridentate in female; apicoventral mandibular tooth of female acute; mandible without inner basal tooth; male clypeal apex unmodified, not bevelled; 3 clypeal teeth in female; interantennal tubercle developed; frontal carina absent; vertex with micropore field undeveloped consisting of only a few associated pits in a puncture-like depression; inner orbits converging below; eyes margined by a

carina; occipital carina present, simple in female, foveolate in male; occipital carina complete, not intersecting hypostomal carina.

Mesosoma. Scutum without median groove; notaular grooves normal, not elongate. Acetabular carina absent, omaulus curving forward toward prothorax. Scrobal sulcus absent to weakly present. Hypoepimeral area without coarse sculpture. Hind tibia with 2 or 3 spines on posterior margin. Mid basitarsus of male as long or longer than next 3 tarsomeres combined. Fore wing setae absent in cellular area. Hind wing media diverging just after cu-a; submedian cell of normal size, not reduced.

Metasoma. Petiole smooth and round, occasionally finely microcarinate. Pygidial plate narrow, present in female only. Digitus elongate, toothed; cuspis not lobed but multitoothed.

Type Species.—*Tzustigmus syam* new species.

Distribution.—Oriental, far eastern Palearctic.

Species Transferred.—*Carinostigmus rhinocerus* Budrys.

KEY TO SPECIES OF TZUSTIGMUS

(Males of *T. rhinocerus* and *T. veda* are unknown)

- 1. Hypoepimeral area with a single ventral carina forming upper margin of scrobal sulcus (Fig. 9); scrobal sulcus foveolate; male fore basitarsus unmodified; female with area adjacent to propodeal enclosure unsculpted at least posterolaterally; south India to Vietnam 3. *syam* Fিন্নমোৰ, new species
- 1'. Hypoepimeral area carinate on ventral half; scrobal sulcus not evident; male fore basitarsus angulate medially; female with area adjacent to propodeal enclosure finely carinate ... 2
- 2. At least dorsal surface of petiole microcarinate; Thailand to Vietnam 1. *khmer* Fিন্নমোৰ, new species
- 2'. Dorsal surface of petiole unsculptured, shiny, dorsolateral sulci may be present 3
- 3. Pronotal transverse sulcus unsculptured; south India 4. *veda* Fিন্নমোৰ, new species
- 3'. Pronotum carinate on transverse sulcus 4
- 4. Sternopleural region closely and finely striatopunctate; Russian Federation: far east 2. *rhinocerus* (Budrys)
- 4'. Sternopleural region shiny, punctate only; Taiwan 5. *wuming* Fিন্নমোৰ, new species

1. **Tzustigmus khmer** Finnamore,
new species

Derivation of Name.—The species epithet, *khmer*, refers to the 11th century invaders of the Dvaravati Kingdom then occupying present day Thailand which is within the distribution range of this species.

Diagnosis.—This species is readily distinguished from its relatives by the microcarinate petiole (at least dorsally).

Description.—Male. Length 4.5 mm.

Head. Flagellomeres without visible tyli. Head shiny, without microsculpture. Clypeus obscured by dense appressed setae that extend along inner orbits to half height of scape. Inner and outer orbit margined by coarsely foveolate sulcus that is absent ventrally and anterodorsally. Frons lower two thirds with irregular, coarse, transverse carinae. Vertex with sparse, evanescent punctures. Ocelli closer to each other than to eye, OOD $1.4 \times$ LOD. Gena with sparse punctures and sparse setae that increase in density ventrally. Occipital carina foveolate, more coarsely so ventrally.

Mesosoma. Pronotum with transverse sulcus longitudinally carinate; side longitudinally carinate. Scutum shiny, sparsely punctate, with anterior transverse microcarinae becoming longitudinal adjacent to admedian lines, posterior edge margined by a transverse row of short carinae. Hypoepimeral area microcarinate on ventral half. Scrobal sulcus not or at most only slightly evident. Sternopleural region shiny, without microsculpture, sparsely punctate. Omaulus and hypersternaulus coarsely foveolate. Scutellum entirely or mostly shiny, without microsculpture anteriorly, but sometimes present posteriorly. Metapleuron carinate. Propodeum with side entirely finely longitudinally carinate, dorsolateral carina evanescent, lateral spheres shiny with microcarinae, enclosure with irregularly areolate sculpture. Fore basitarsus angulate at basal third.

Metasoma. Petiole round, longitudinally microcarinate dorsally and laterally, ventrolateral carinae faintly indicated posteriorly. Terga II–V usually with large sparse punctures in a more or less transverse median band. Sterna IV–VI with apical band of dense punctures up to one puncture diameter apart, apical margins impunctate. Metasoma with microsculpture so fine as to impart an oily sheen that is most evident on the terga.

Color. Ground color black. White: pronotal lobe. Brown to yellow-brown: mandible, palpi, antenna, legs, except coxae, tegula, stigma.

Female. Length 5 mm. Similar to male except as follows: clypeus sparsely setose, underlying sculpture visible, punctures sparse and up to several diameters apart on median area which is slightly bulging. OOD $2.3 \times$ LOD. Body sculpture stronger than in male, punctation closer than in male particularly on sternopleural region where fine punctures are evenly distributed up to 2 diameters apart. Mesopleuron longitudinally carinate from dorsal hypoepimeral area to hypersternaulus. Fore basitarsus straight, not angled at basal third. Petiole round, entirely microcarinate. Abdominal tergum VI with narrow, shiny, impunctate pygidial plate.

Material Examined (2♂, 2♀).—Holotype: ♂, VIET NAM: 15 km nw. of Dalat [Da Lat], 1850 m, 5-V-1960. L.W. Quate (BISH). Paratypes: **THAILAND: Chiangmai:** Doi pui, 2-IV-1958. T.C. Maa (♂: 1 BISH). **VIETNAM:** Fyan, 1200 m. 11-VII-9-VIII-1961. N.R. Spencer (♀: 1 BISH). **VIETNAM:** Mt. Lang Bian, 1500–2000 m. 19-V-8-VI-1961. N.R. Spencer (♀: 1 BISH).

Distribution (Map 1).—Thailand to Vietnam.

2. **Tzustigmus rhinocerus** (Budrys),
new combination

Carinostigmus rhinocerus Budrys 1987:54, ♀, ♂. Holotype: ♀ (not examined), Russian Federation: Khabarovsk, Khlekhtsir Range, Levaya River (ZIN).

Diagnosis.—The combination of a hypoepimeral area carinate on ventral half, sternopleural region closely and finely striatopunctate, propodeum with carinate lateral spheres and petiole shiny without microcarinae (dorsolateral carinae are faintly indicated) separate this species from others in the genus.

Description.—Male. Not seen.

Female. Length 6.5 mm.

Head. Clypeus with relatively long decurved setae, not obscuring underlying sculpture, punctures coarse and contiguous on median area which is strongly bulging. Inner and outer orbit margined by a coarsely foveolate sulcus which is absent ventrally and anterodorsally. Frons irregularly, transversely carinate adjacent to lower inner orbit becoming striatopunctate toward vertex. Scapal basin dull, densely microsculptured. Vertex shiny anteriorly, obscurely striatopunctate, punctures sparse with most over 3 diameters apart; posterior vertex with transverse microsculpture. Lateral ocelli closer to each other than to eyes, OOD $2.6 \times$ LOD. Gena striatopunctate, more densely so ventrally. Occipital carina simple, not foveolate.

Mesosoma. Pronotum with transverse sulcus longitudinally carinate; side longitudinally carinate. Scutum shiny, sparsely punctate, with anterior transverse microcarinae that become longitudinal adjacent to admedian lines, posterior edge margined by transverse row of short carinae. Mesopleuron longitudinally carinate from dorsal part of hypoepimeral area to hypersternaulus (which is coarsely foveolate). Sternopleural region shiny with dense, fine punctures (that are less than 1 diameter apart), somewhat finely striatopunctate toward posterior. Omaulus foveolate. Scutellum shiny anteriorly, sparsely punctured, microsculptured on posterior third. Metapleuron longitudinally carinate. Propodeal side longitudinally carinate throughout; dorsolateral carina present, irregular; lateral spheres carinate to propodeal enclosure which is irregularly areo-

late. Fore basitarsus straight, subcylindrical, not bent or otherwise modified.

Metasoma. Petiole round, shiny with dorsolateral carina partially developed anteriorly. Terga II–V with medium size, widely scattered sparse punctures; microsculpture on anterior terga imparts an oily sheen to metasoma. Sterna IV and V with apical bands of punctures, punctures at least 2 diameters apart; sternum VI with close nearly contiguous punctures.

Color. Ground color black. White: pronotal lobe. Brown to yellow-brown: mandibles except apex, palpi, scape, underside of flagellum, legs except coxae and hind femur, tegula, pygidial plate.

Material Examined (1♀ paratype).—**RUSSIAN FEDERATION: Khabarovsk:** Khekhtsir, 18th km.

Distribution (Map 2).—Russian Federation far east.

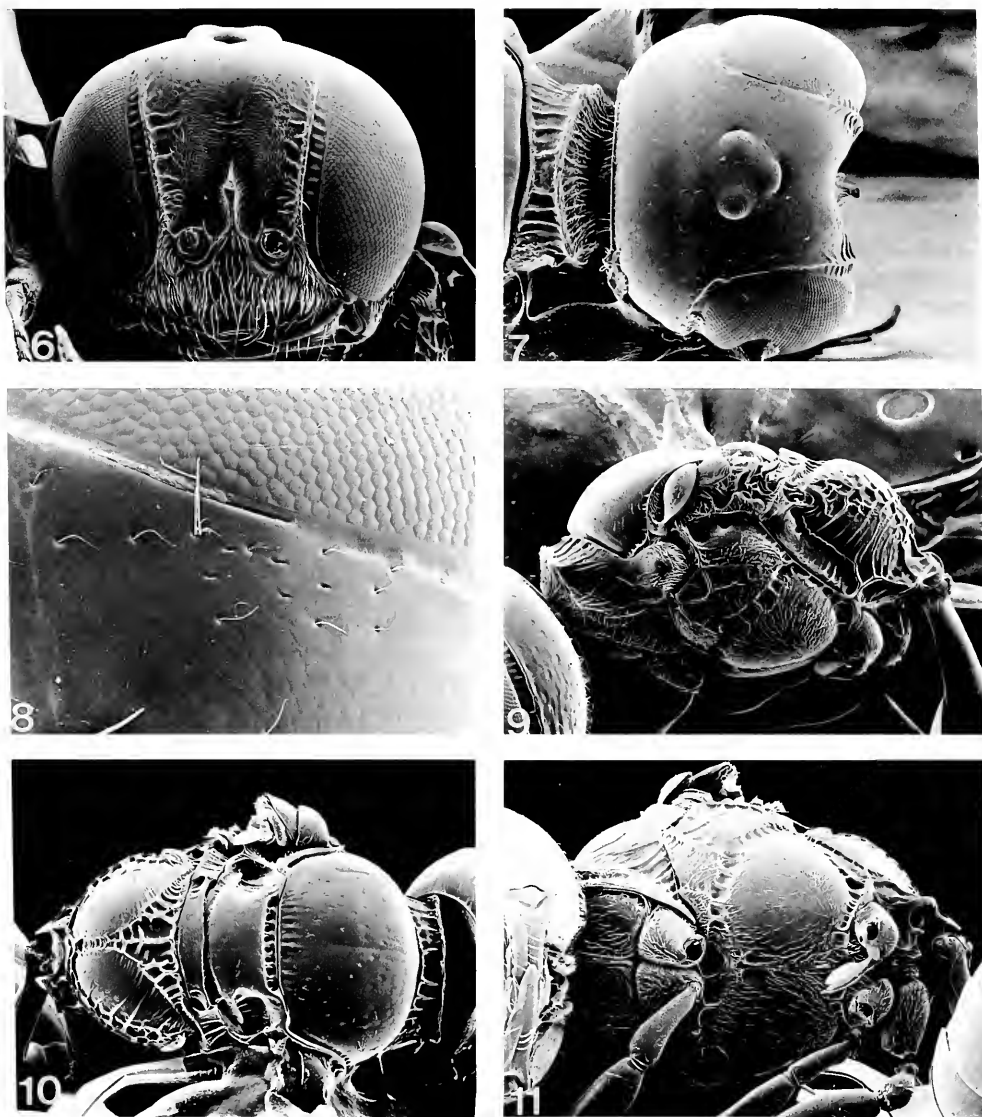
3. *Tzustigmus syam* Finnamore, new species

Derivation of Name.—The species epithet, *syam*, is a sanskrit term for dark used by 12th century Khmers to refer to the dark skin of the people migrating south from southern China at that time. It is used here to refer to the generally dark appearance of this species.

Diagnosis.—The unsculpted (non-carinate) hypoepimeral area will distinguish this species from others in the genus.

Description.—Male. Length 4 mm.

Head. Flagellomeres without tyli. Head shiny with microsculpture on frons, gena and posterior vertex. Clypeus obscured by dense appressed setae which extend along inner orbits to a point $\frac{1}{4}$ height of scape. Inner and outer orbit margined by a coarsely foveolate sulcus except ventrally and dorsally. Frons microsculptured, without carinae except along inner orbital margin where they are evanescent. Vertex sparsely punctate, with minute punctures, appearing impunctate. Ocelli closer to each other than to eyes; OOD $1.4 \times$ LOD.



Figs. 6-11. *Tzutigmus syam* ♀. 6, head, frontal view. 7, head and prothorax, dorsal view. 8, micropore field between lateral ocellus and compound eye. 9, mesosoma, lateral view. 10, mesosoma, dorsal view. 11, mesosoma, ventrolateral view.

Gena almost impunctate, with microsculpture present to absent. Occipital carina foveolate, areolae becoming evanescent dorsally.

Mesosoma. Pronotum with transverse sulcus longitudinally carinate; side longitudinally carinate. Scutum shiny, sparsely punctate, without anterior microcarinae; with transverse row of short longitudinal

carinae next to posterior margin. Hypopimeral area microsculptured, not carinate; scrobal sulcus distinct, carinate and foveolate. Sternopleural region shiny, without microsculpture, sparsely micropunctate. Omaulus and hypersternaulus coarsely foveolate. Scutellum shiny, with several punctures mediolaterally. Metapleuron not carinate. Propodeal side with

evanescent carinae, less so in the discal area; dorsolateral area a series of areolae, lateral spheres shiny, weakly carinate basally becoming evanescent and absent toward midline; propodeal enclosure areolate. Fore basitarsus straight, cylindrical.

Metasoma. Petiole round, shiny, without microsculpture or dorsolateral carina. Terga impunctate (this character is variable in other species and as more specimens are encountered may prove to be punctate in some specimens). Sterna IV to VI with apical bands of small punctures less dense than in previous species. Terga with fine microsculpture so as to impart an oily sheen.

Color. Ground color black. White: pronotal lobe. Brown to yellow-brown: mandibles except apically, palpi, antenna, tegula, legs.

Female. Length 4.5 mm. Similar to male except as follows: clypeus with 3 median teeth, sparsely setose, underlying sculpture visible medially; median area bulging but not strongly so and shiny with punctures 1.5 to 3 diameters apart. OOD $2.6 \times$ LOD. Occipital carina not as strongly areolate. Gena striatopunctate ventrally. Propodeal side more strongly carinate than in male. Tergum VI with a narrow shiny pygidial plate.

Material Examined (2♂, 8♀).—**Holotype:** ♀, THAILAND: Chiangmai Prov., 10 km w. Fang, V-5-69, G.R. Ballmer, on tree trunk (PMA). **Paratypes:** **INDIA: Karnataka:** Bangalore, 916 m, 9-XII-1973, Ghorpade collection, Bangalore (♀: 1 ZMD). Nilgiri Hills, Naduvattam, 6000 ft. May 1958, P.S. Nathan. George R. Ferguson Collection, 1972 (♂: 1 OSU). **THAILAND: Chiangmai:** 10 km w. Fang, 5-V-69, G.R. Ballmer, on tree trunk (♀: 2 PMA). Doi Suthep-Pui natn. Park, Konthathan waterfall area, 600 m, 20-27-X-1979. Zool. Mus. Copenhagen Exped. (♀: 1 ZMD). **VIETNAM:** Dalat [Da Lat] 6 km s., 1400–1500 m, 9-VI-7-VII-1961, N.R. Spencer, ♀: 1 BISH. Fyan, 900–1000 m. 11-VII-9-VIII-'61, N.R. Spencer (♀: 1 BISH). Fyan, 1200 m.

11-VII-9-VIII-'61, N.R. Spencer (♀: 1 BISH, ♂: 1 BISH). The male was collected at a light trap.

Distribution (Map 3).—India to Vietnam.

4. *Tzustigmus veda* Finnamore, new species

Derivation of Name.—The species epithet was arbitrarily selected for the species. Veda, in Hindu perspective is the eternal wisdom realized by the ancient seers or sages preserved over thousands of years by generations of professional reciters in oral transmission.

Diagnosis.—The non-carinate, smooth, transverse pronotal sulcus is diagnostic for this species.

Description.—Male unknown.

Female. Length 4.5 mm.

Head. Head shiny, faint microsculpture on frons and posterior vertex. Clypeus with 3 median teeth, sparsely setose, underlying sculpture visible medially, shiny, closely punctate, punctures 1–2 diameters apart. Inner and outer orbit margined by a coarsely foveolate sulcus except ventrally and dorsally. Frons with fine transverse microcarinae and some coarse transverse carinae near inner orbital sulcus. Vertex shiny with fine microsculpture posteriorly, punctures fine, sparse. Lateral ocelli closer to each other than to eyes, OOD $1.9 \times$ LOD. Gena shiny, sparsely punctate dorsally, closely punctate to striatopunctate ventrally. Occipital carina simple, obscurely foveolate ventrally.

Mesosoma. Pronotum with transverse sulcus unsculptured although longitudinal carinae are present at extreme dorsolateral end, side longitudinally carinate. Scutum shiny, sparsely punctate, with fine anterior transverse microcarinae that turn longitudinally adjacent to admedian lines; with transverse row of short carinae next to posterior margin. Hypoepimeral area carinate over most of its area. Scrobal sulcus evanescent. Omaulus and hypersternaulus foveolate. Sternopleural region shiny, without microsculpture, punctures

fine 1–2 diameters apart. Scutellum shiny anteriorly, posterior $\frac{2}{3}$ microsculptured and sparsely punctate. Metapleuron carinate. Propodeum carinate laterally, dorsolateral carina present, lateral spheres finely carinate to propodeal enclosure which is areolate.

Metasoma. Petiole round, shiny, without microsculpture, dorsolateral carina faintly indicated anteriorly. Terga with few fine evanescent punctures and with microsculpture imparting oily sheen. Sterna III–V with sparse bands of punctures, VI closely punctate, punctures less than 1 diameter apart near apex.

Color. Ground color black. White: pronotal lobe. Brown to yellow-brown: mandibles except apex, palpi, scape, tegula, legs.

Material Examined (1♀).—Holotype: ♀, S. INDIA: Cinchona, Anamalai Hills [Anaimalai], 3500 ft. May 1959, P.S. Nathan. George R. Ferguson Collection (OSU).

Distribution (Map 4).—Southern India.

5. *Tzustigmus wuming* Finnamore, new species

Derivation of Name.—The species epithet, *wuming*, is a Chinese term derived from Taoist philosophy referring to that which is unnameable.

Diagnosis.—Resembling *T. rhinocerus* in having the hypopimeral area carinate on ventral half, the propodeum with closely carinate lateral spheres, and the petiole shiny without microcarinae. Unlike *rhinocerus*, *wuming* has a smooth, shiny, sparsely punctate sternopleural region. Additionally the pleuron of *wuming* is unsculptured immediately above hypersternaulus, while in *rhinocerus* it is sculptured from the mid hypopimeral area to hypersternaulus and sternopleural region.

Description.—Male. Length 4 mm.

Head. Flagellomeres without tyli. Head shiny with microsculpture on frons, vertex and occasionally gena. Clypeus obscured by dense, appressed setae which extend along inner orbits to about half height of

scape. Inner and outer orbits margined by a coarsely foveolate sulcus except ventrally and dorsally. Frons microsculptured on scapal basin, elsewhere with relatively coarse, irregularly transverse carinae which meet dorsally. Vertex sparsely punctate with minute punctures. Ocelli closer to each other than to eyes; OOD 1.8 × LOD. Gena sparsely punctate dorsally, more densely punctate ventrally; microsculpture present to absent. Occipital carina foveolate.

Mesosoma. Pronotum with transverse sulcus longitudinally carinate; side longitudinally carinate. Scutum shiny, sparsely punctate; with transverse anterior microcarinae that turn longitudinally adjacent to admedian lines; posterior edge margined by a transverse row of short carinae. Hypopimeral area carinate. Scrobal sulcus indistinct, carinae not extending ventrally to hypersternaulus. Sternopleural region shiny, without microsculpture, sparsely and obscurely punctate. Omaulus and hypersternaulus coarsely foveolate. Scutellum shiny, without microsculpture except faintly microsculptured on posterior third; sparsely punctate. Metapleuron carinate on ventral half. Propodeal side carinate, dorsolateral area with slightly more coarse irregular sculpture, lateral spheres carinate; propodeal enclosure areolate. Fore basitarsus angulate at basal third.

Metasoma. Petiole round, shiny, without microsculpture or dorsolateral carina except remnant anteriorly. Terga sparsely, obscurely punctate. Sterna III–VI with broad bands of punctures most of which are less than 1 diameter apart. Terga with fine microsculpture imparting oily sheen.

Color. Ground color black. White: pronotal lobe. Brown to yellow-brown: palpi, antenna, legs except coxae, tegula, stigma.

Female. Length 5–6 mm. Similar to male except as follows: clypeus sparsely setose, underlying sculpture visible on median area, punctures sparse (1–2 diameters apart) on median area which is slightly

bulging, with 3 weakly developed apical teeth. Frons with irregular transverse carinae not as strong as in male and sometimes evanescent dorsally on midline. OOD 2.2–2.3 × LOD. Sternopleural region slightly more densely punctate than in male, punctures pin prick fine. Fore basitarsus straight, not angulate. Abdominal tergum VI with narrow shiny pygidial plate. Mandibles yellow-brown.

Material Examined 2♂, 4♀).—Holotype: ♀, TAIWAN: Wushe, 1150 m, III-16-'83, H. & M. Townes (AEI). Paratypes: **TAIWAN**: Wushe, 1150 m, III-23-'83, H. & M. Townes. 1150 m (♂: 1 AEI). Wushe, IV-2–83, Henry Townes (♀: 1 AEI). Wushe, 1150 m, IV-19–83, Henry Townes (♀: 1 AEI). Wushe, 1150 m, IV-26–83, Henry Townes (♂: 1 AEI). Wushe, 1150 m, V-3–83, Henry Townes (♀: 1 AEI).

Distribution.—(Map 5). Taiwan.

PARASTIGMUS Antropov

Parastigmus Antropov 1992:97. Type species *Parastigmus argentinus* Antropov, 1992, by original designation and monotypy.

Diagnosis.—The combination of a microsculptured body, the hind wing media diverging just before cu-a, a broad pygidial plate, and the lack of an acetabular carina will separate this genus from others in the Stigmina.

Description.—Head. Labrum quadri-lobed, with median emargination narrow and deep. Mandible with apex bidentate

in both sexes; apicoventral tooth of female acute; inner basal tooth in at least females of some species. Clypeal apex in male without bevelled modifications; 4 clypeal teeth present in female, although median teeth are often fully reduced imparting a deep, broad, median emargination. Inter-antennal tubercle absent. Frontal carina absent in male, present but simple in female. Vertex without micropore field. Inner orbits parallel in female, converging below in male. Eye not margined by a carina. Occipital carina simple, complete, not intersecting hypostomal carina.

Mesosoma. Scutum without median groove; notaular groove normal, short, not elongate. Acetabular carina absent; omaulus curving forward toward prothorax. Scrobal sulcus absent in male, evanescent in female. Hypoepimeral area without coarse sculpture. Mid basitarsus in male unmodified, as long as or longer than next 3 tarsomeres combined. Hind tibia with 2 or 3 spines on posterior margin. Fore wing without setae in cellular area. Hind wing media diverging before cu-a; submedian cell of normal size, not reduced.

Metasoma. Petiole carinate. Pygidial plate broad, present in both sexes. Digitus elongate, toothed; cuspis not lobed, toothed.

Distribution (Map 34).—Southern Neotropical.

Species Transferred.—*Stigmus patagonicus* Mantero.

KEY TO SPECIES OF *PARASTIGMUS*

| | |
|--|---|
| 1 Males | 2 |
| 1' Females | 5 |
| 2 Mesosoma entirely dull, microsculptured; Chile | 2. <i>huecuvus</i> Finnamore, new species |
| 2' Scutellum or sternopleural region shiny, without microsculpture; Argentina | 3 |
| 3 Sternum II and apices of terga I and II, red | 1. <i>argentinus</i> Antropov |
| 3' Metasoma all black | 4 |
| 4 Pedicel subequal to length of first flagellomere (1:1) | 4. <i>patagonicus</i> (Mantero) |
| 4' Pedicel longer than first flagellomere (1:0.7) | 3. <i>nina</i> Finnamore, new species |
| 5 Apex of clypeus transverse with 4 small equally developed teeth; labrum not exposed; Chile | 2. <i>huecuvus</i> Finnamore, new species |

- 5' Apex of clypeus with a broad, deep median emargination or biemargination exposing labrum; lateral teeth prominent; median lobe present or absent; Argentina 6
- 6 Pedicel longer than first flagellomere (1:0.6–0.7); mesosoma red or black 3. *nina* Finnamore, new species
- 6' Pedicel subequal to length of first flagellomere (1:0.9–1.1); mesosoma black 7
- 7 Clypeus biemarginate, median lobe developed; clypeus and inner orbits bare, without appressed setae 1. *argentinus* Antropov
- 7' Clypeus with single broad median emargination, median lobe evanescent or absent; clypeus and inner orbits with appressed setae that partially obscure surface 4. *patagonicus* (Mantero)

1. *Parastigmus argentinus* Antropov

Parastigmus argentinus Antropov 1992:99 ♀. Holotype: ♀ (not examined), ARGENTINA: Neuquén, Collón Curá, 19-I-1980. Willink, Fidalgo, Dominguez, Claps (LILLO).

Diagnosis.—The male is recognized by its red metasomal sternum II, longitudinally microsculptured scutum, and length of flagellomere I which is $0.75 \times$ length of pedicel. Males of other species have a first flagellomere length subequal to pedicel and/or microsculpture of scutum demonstrating no particular orientation. The metasoma of other species is black and may also prove to be black in other specimens of this species. The female is recognized by its biemarginate clypeal edge with median lobe developed.

Description.—Male. Length 3.5 mm.

Head. Flagellomeres without tyli. Ratio of pedicel to flagellomere I is 1:0.75. Head coarsely microsculptured, without shiny areas. Clypeus and subantennal area obscured by dense appressed setae which extend broadly up the inner orbits to a point $1.6 \times$ scapal length. Frons and vertex with sparse obscure punctures, appearing impunctate at low magnification. Ocelli closer to each other than to eyes; OOD $1.6 \times$ LOD. Genal punctures evanescent.

Mesosoma. Pronotum with transverse sulcus longitudinally carinate. Scutum longitudinally microsculptured; scutellum and mesopleuron above hypersternaulus microsculptured; sternopleural region

somewhat shiny, weakly microsculptured. Scutum without appressed setae; punctures sparse, evanescent; notaular grooves foveolate. Scutellum sparsely punctate, punctures evanescent. Scrobal sulcus absent. Mesopleuron impunctate. Hypersternaulus and omaulus weakly foveolate. Metapleuron shiny, weakly microsculptured. Propodeum with areolate sculpture over most of surface, sculpture finer toward metapleuron; dorsal enclosure not defined by a carina.

Metasoma. Microsculptured, punctate at apices of terga II–VI, more coarsely so on posterior terga; terga V and VI sparsely punctate over entire dorsal area. Tergum VII with ill-defined pygidial plate, punctured, shiny, impunctate apically. Setal density abruptly increasing on tergum IV to posterior metasoma.

Color. Ground color black. White: palpi, labrum, mandible except apex, scape ventrally, pronotal lobe, anterior spot on tegula. Brown to yellow-brown: antenna except ventral scape, fore leg beyond coxa, mid leg beyond coxa, hind leg except coxa and femur, tegula except anterior spot, stigma. Red: apices of metasomal terga I and II, sterna II, base of III and VII.

Female. Length 4 mm. Similar to male except as follows: ratio of pedicel to flagellomere I is 1:1.1. Clypeus almost devoid of setae and punctures, shiny, without microsculpture; apex biemarginate with lateral teeth prominent and median lobe developed. Inner orbits with several setae that do not obscure underlying

sculpture. Subantennal area without setae. Frons somewhat shiny, with weak microsculpture. Vertex posterior to ocelli, transversely microsculptured. OOD $2.2 \times$ LOD. Upper frons and vertex sparsely punctate. Lower gena more densely punctate than upper gena, punctures 1–2 diameters apart near mandibular base. Scutum sparsely punctate. Mesopleuron shiny, without microsculpture; scrobal sulcus slightly impressed; sternopleural region closely punctate, punctures minute, 1–3 diameters apart. Pygidial plate broad, shiny, punctate on midline, more broadly punctate basally. Colored as in male but without red.

Material Examined (1♂, 1♀).—**ARGENTINA: Neuquén:** Collón Curá, 19-I-1980. Willink, Fidalgo, Dominguez, Claps.

Distribution (Map 6).—Argentina.

2. *Parastigmus huecuvus* Finnamore, new species

Derivation of Name.—Huecuvue, from Araucanian mythology (Chile), are spirits able to change into any form they wished for the purpose of doing evil, in this case creating confusion among taxonomists due to aberrant characters.

Diagnosis.—Males are distinguished from other *Parastigmus* by the entirely microsculptured mesosoma and black abdomen. Other species have a shiny sternopleural region, and the metasoma is in part red in *patagonicus*. The female is unique in the genus in having 4 subequally developed clypeal teeth and without a broad median emargination. The clypeus in females of other species has a broad median emargination in which the median teeth or lobe is recessed or absent resulting in prominent lateral teeth.

Description.—Male. Length 3.5 mm.

Head. Flagellomeres without tyli. Ratio of pedicel to flagellomere I is 1:0.9. Head entirely microsculptured. Clypeus and subantennal area obscured by dense appressed setae which extend along inner orbits to a point 1.5 times length of scape.

Punctures of frons and vertex sparse, evanescent. Ocelli closer to each other than to eyes; OOD $1.4\text{--}1.6 \times$ LOD. Genal punctures evanescent.

Mesosoma. Entirely microsculptured. Pronotum with transverse sulcus longitudinally carinate; pronotal side longitudinally carinate. Scutum and scutellum sparsely punctate, with many large impunctate areas; microsculpture simple, not oriented in any direction. Notaular grooves deeply impressed, coarsely foveolate. Scrobal sulcus absent. Mesopleuron impunctate, without carinae except occasionally at lower posterior margin. Omaulus and hypersternaulus foveolate. Metapleuron microsculptured, without carinae, impunctate. Propodeal sculpture irregularly areolate on dorsal and posterior surface. Propodeal enclosure not evident. Propodeal side with sculpture evanescent toward metapleuron.

Metasoma. Microsculptured except tergum VII. Punctures of terga and sterna small, sparse, evanescent. Pygidial plate shiny medially, without microsculpture, 2 or 3 punctures laterally. Setal density increasing toward posterior metasoma.

Color. Ground color black. White: Mandible except apex, scape ventrally, pronotal lobe, anterior spot on tegula. Brown to yellow-brown: palpi, antenna except ventral scape, stigma, legs but coxae and femora tend to be darker brown and fore leg tends to be lighter yellow-brown.

Female. Length 4 mm. Similar to male except as follows: clypeus entirely, evenly setose although setae not obscuring underlying surface, shiny, microsculpture absent, with several relatively large punctures subapically along apex. Clypeal apex with 4 subequally developed teeth, without a broad median emargination. Subantennal area and inner orbits without setae. OOD $2 \times$ LOD. Pygidial plate shiny, impunctate over lateral third; median third slightly raised, shiny, without microsculpture, irregularly punctate and irregularly, finely rugose.

Material Examined (3♂, 10♀).—Holotype: ♀, CHILE: Santiago—Cordillera, Reserva Río Clarillos 1–20-II-1989. R. Miller & L. Stange. Malaise Trap (FSCA). Paratypes: **CHILE: Concepción:** Concepc. 19/12 1907. P. Herbst (♀: 1 NMW). The 19/12 and the 7 in 1907 are inscribed in red ink on the specimen label, in the latter case the 7 is written over the 4 in 1904. Specimen bears a second label with the numbers 17 and 84. Concepc. 27/12 1907. P. Herbst (♂: 2 NMW). The 27/12 and the 7 are inscribed in red ink on the specimen label in the latter case the 7 in 1907 is written over the 3 in 1903 or the 4 in 1904. Concepc. 3–1908. P. Herbst (♂: 1 NMW). The 3 and 8 are inscribed in red ink, the latter over the 4 in 1904. **Santiago:** Cordillera, Reserva Río Clarillos 1–20-II-1989. R. Miller & L. Stange. Malaise Trap (♀: 5 FSCA, 2 PMA). Cordillera, Reserva Río Clarillos 21–28-II-1989. R. Miller & L. Stange. Malaise Trap (♀: 1 FSCA).

Distribution.—(Map 7). Chile.

3. *Parastigmus nina* Finnamore, new species

Derivation of Name.—Nina is a Quechua term meaning fire, referring to the red mesosoma of the holotype.

Diagnosis.—The short flagellomere I ($0.6\text{--}0.7 \times$ length of pedicel) distinguishes this species from others in the genus except males of *argentinus*. In all other species the length of flagellomere I equals $0.9\text{--}1.1$ of the pedicel length, except male of *argentinus* which differs from *nina* in its red second metasomal sternum. *Parastigmus nina* has a pedicel:flagellomere I ratio of $1:0.6\text{--}0.7$, black metasoma, and the mesosoma may be red or black, that of the female holotype is extensively red.

Description.—Male. Length 4 mm.

Head. Flagellomeres without tyli. Ratio of pedicel to flagellomere I is $1:0.7$. Head microsculptured except near frontal carina where microsculpture is evanescent. Clypeus and subantennal area obscured by dense appressed setae which extend

broadly up the inner orbits to a point almost twice the length of the scape. Frons and vertex irregularly punctate ($1\text{--}5$ diameters apart). Ocelli slightly closer to each other than to eyes; $OOD\ 1.5 \times LOD$. Genal punctures evanescent.

Mesosoma. Scutum, scutellum, mesopleuron, and upper metapleuron extensively shiny, microsculptured in part. Pronotum with transverse sulcus longitudinally carinate; side weakly carinate. Anterior quarter of scutum partially obscured by dense appressed setae, microsculptured; median and posterior areas of scutum shiny with evanescent microsculpture, punctures sparse, notaular grooves foveolate. Scutellum shiny, sparsely punctate anteriorly, microsculptured posteriorly. Scrobal sulcus absent. Mesopleuron immediately ventral to hypersternaulus, minutely punctured; elsewhere punctures sparse, evanescent. Hypersternaulus and omaulus weakly foveolate. Mesopleuron microsculptured posteriorly, mostly shiny anteriorly. Metapleuron microsculptured over most of surface except dorsal shiny patch. Propodeum coarsely microsculptured on side, finely areolate dorsally, posteriorly, and on lateral sphere. Propodeal enclosure not defined by a carina.

Metasoma. Microsculptured, impunctate except tergum VII. Sterna II–IV minutely punctate posteriorly. Pygidial plate ill-defined, shiny medially, without microsculpture, several punctures present laterally. Setal density gradually increasing toward posterior metasoma.

Color. Ground color black. White: mandible except apex, labrum, scape ventrally, pronotal lobe, anterior spot on tegula. Brown to yellow-brown: palpi, antenna except ventral scape, stigma, legs except coxae, hind leg is darker than other legs.

Female. Length $4.0\text{--}4.5$ mm. Similar to male except as follows: ratio of pedicel to flagellomere I is $1:0.6\text{--}0.7$. Clypeus sparsely setose, shiny, sparsely punctate with median bulge; apex broadly and deeply emarginate over median 0.45 ; lateral teeth

acute, prominent; median teeth absent. Inner orbits and subantennal area not setose. OOD $2.3 \times$ LOD. Mesosoma red or black, the holotype has a red mesosoma with black in the following areas: propodeal enclosure, mid ventral line, coxae, mid trochanter, mid femur, hind leg; otherwise colored as in the male. The ♀ paratype has the same color pattern as the male. Pygidial plate broad, shiny, sparsely punctate medially.

Material Examined (1♂, 2♀).—Holotype: ♀, ARGENTINA: Neuquén, Collón Curá 19-I-1980. Willink, Fidalgo, Dominguez, Claps (LILLO). Paratypes: ARGENTINA: Neuquén: Collón Curá 19-I-1980. Willink, Fidalgo, Dominguez, Claps (♂: 1 LILLO). Santa Cruz: 3 km s. Río Chico at Hwy. 3; XII-11-1966, 90m, E.I. Schlinger & M.E. Irwin (♀: 1 CAS).

Distribution (Map 8).—Argentina.

4. *Parastigmus patagonicus* (Mantero) new combination

Stigmus patagonicus Mantero 1901:199 ♂. Holotype*: ♂, Río Sta. Cruz, Silvestri (MCSN).

Diagnosis.—The male can be distinguished from all other species in the genus by the combination of a pedicel subequal to length of flagellomere I, and a shiny mesopleuron without microsculpture ventral to hypopleural area. The male of this species is superficially similar to *huecuvus* with which it shares a long first flagellomere. In addition to the mesopleural microsculpture the length of the petiole may be used to separate the two species; the petiole slightly shorter than tergum I in *huecuvus* and slightly longer than tergum I in *patagonicus*. The petiole length should be used with caution since it is subject to variation in closely related genera and has been excluded from descriptions for that reason. The number of specimens available for this genus is insufficient to determine variation in petiole length.

Females can be separated from other species in the genus by the combination of

the pedicel subequal in length to flagellomere I, and the broadly emarginate clypeus with prominent lateral teeth but without a median lobe.

Description.—Male. Length 4.5–5.0 mm.

Head. Flagellomeres without tyli. Ratio of pedicel to flagellomere I is 1:1. Head coarsely microsculptured, without shiny areas. Clypeus and subantennal area obscured by dense appressed setae which extend broadly up inner orbit to a point $1.5 \times$ length of scape. Upper frons and lower gena sparsely punctate. Ocelli closer to each other than to eye. OOD $1.6\text{--}1.7 \times$ LOD.

Mesosoma. Pronotum with transverse sulcus longitudinally carinate. Scutum and scutellum microsculptured, without appressed setae, sparsely punctate; notaular grooves foveolate. Mesopleuron shiny, without microsculpture ventral to hypopleural area which has evanescent microsculpture (may be longitudinally oriented). Punctures on sternopleural region minute, 3–4 diameters apart. Scrobal sulcus absent, indicated only by change in microsculpture. Hypersternaulus and omaulus weakly foveolate. Metapleural microsculpture evanescent. Propodeum microsculptured, areolate over most of surface except near metapleuron where it is carinate; propodeal enclosure not indicated by a carina.

Metasoma. Metasoma microsculptured except tergum VII, punctures evanescent but more evident on apices of apical terga. Pygidial plate ill-defined, shiny, sparsely punctate. Setal density gradually increasing toward posterior of metasoma.

Color. Ground color black. White: palpi, labrum, mandible except apex, scape ventrally, pronotal lobe, anterior spot on tegula. Brown to yellow-brown: antenna except scape ventrally, fore leg, mid leg, hind leg except coxa and femur, tegula except anterior spot.

Female. Length 6.0–6.5 mm. Similar to male except as follows: clypeus evenly covered with dense setae that partially ob-

scure sculpture beneath and extend up inner orbit to a point subequal to length of scape. Clypeus without microsculpture, shiny, punctures minute and sparse. Clypeal apex broadly emarginate, lateral teeth prominent, median lobe (teeth) reduced to a small mid point. Subantennal area without setae. OOD $1.8-1.9 \times$ LOD. Mesosoma with scrobal sulcus slightly more impressed than in male. Propodeum more coarsely areolate than male. Pygidial plate broad, shiny with submedian puncture row that converges apically with the median.

Material Examined (5♂, 2♀).—**ARGENTINA: Catamarca:** Andahuallas 2000m. **Santa Cruz:** Río Santa Cruz (Type locality). **Tucuman:** Amaicha. Amaicha del Valle 1900m.

Distribution (Map 9).—Argentina.

ARAUCASTIGMUS Finnamore,
new genus
(Figs. 12–15)

Derivation of Name.—The genus is named after the Araucanian people of Chile the country of origin of most known specimens.

Diagnosis.—The combination of an acetabular carina present, hind wing media diverging just before cu-a and the mesosoma (except propodeum) without microsculpture will separate this genus from all others in the Stigmina.

Description.—Head. Labrum quadri-

lobed with a narrow deep median emargination. Mandible with apex bidentate in male, tridentate in female; apicoventral tooth acute in female; inner basal tooth absent. Clypeal apex in male without bevelled modification, in female with 4 teeth. Interantennal tubercle absent. Frontal carina present, simple. Vertex with micropore field present, diffuse. Inner orbits converging below. Eye not margined by a carina. Occipital carina present, simple, complete, and separated from hypostomal carina.

Mesosoma. Scutum without median groove, notaular grooves normal, short, not elongate. Acetabular carina absent, omaulus curving forward toward prothorax. Scrobal sulcus absent. Hypoepimeral area without coarse sculpture. Mid basitarsus of male unmodified, as long or longer than next 3 tarsomeres combined. Hind tibia with 2 or 3 spines on posterior margin. Fore wing with setae in cellular areas. Hind wing media diverging before cu-a; submedian cell of normal size, not reduced.

Metasoma. Petiole carinate. Pygidial plate narrow, absent in male. Digitus somewhat elongate; cusps with a large lobe bearing several teeth.

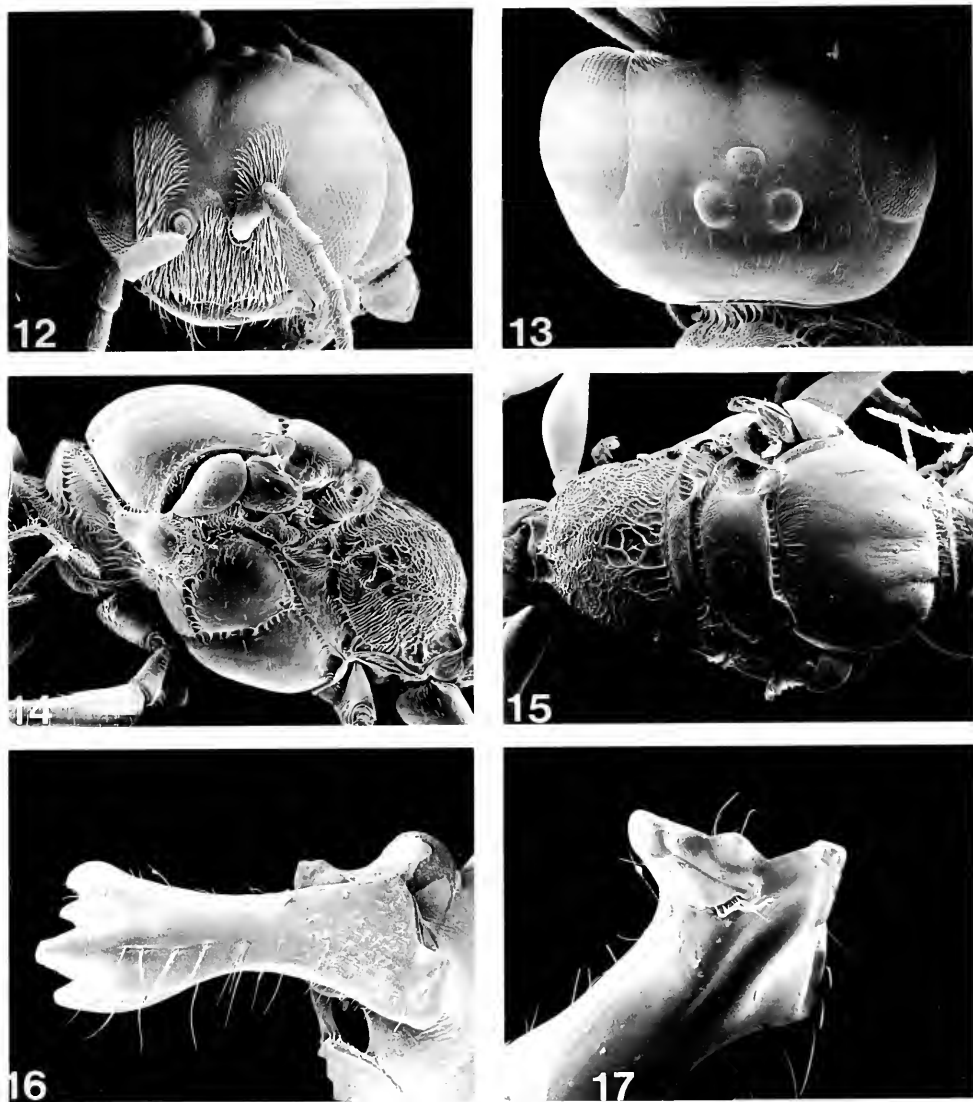
Type Species.—*Araucastigmus glabratus* (Kohl), new combination.

Distribution (Map 35).—Southern Neotropical: Chile.

Species Transferred.—*Stigmus glabratus* Kohl.

KEY TO SPECIES OF ARAUCASTIGMUS

- 1 Propodeum sculptured throughout, area adjacent to metapleuron microsculptured (Figs. 14, 15) 2. *masneri* Finnamore, new species
- 1' Propodeal side with basal shiny area adjacent to metapleuron 2
- 2 Propodeum microsculptured, shiny without microsculpture along mid dorsal line (outside enclosure) in male and also on mid posterior line in female 3. *yanillus* Finnamore, new species
- 2' Propodeum with sculpture in addition to microsculpture at least on dorsolateral areas in male; female without shiny areas on propodeum other than adjacent to metapleuron . . . 1. *glabratus* (Kohl)



Figs. 12–17. *Araucastigmus* and *Paracrabro*. 12, *Araucastigmus masneri* ♂, head, frontal view. 13, *A. masneri* ♂, head, dorsal view. 14, *A. masneri* ♂, mesosoma, lateral view. 15, *A. masneri* ♂, mesosoma, dorsal view. 16, *Paracrabro froggatti* ♀, mandible, outer view. 17, *Paracrabro froggatti* ♀, mandible, inner view.

1. *Araucastigmus glabratus* (Kohl),
new combination

Stigmus glabratus Kohl 1905:358 ♀. Holotype*:
♀, CHILE: Corral [Coul?], 3–1904, P. Herbst
(NMW).

Diagnosis.—Propodeum with shiny area
adjacent to metapleuron and with both
microsculpture and sculpture at least on
dorsolateral areas. Other species are either

microsculptured throughout or macro-
sculpture is absent or shiny areas are
much more extensive.

Description.—Male. Length 3.2–5 mm.

Head. Flagellomeres without tyli. Head
shiny, mostly without microsculpture,
sparsely punctate. Clypeus, subantennal
area and inner orbit obscured by dense
appressed setae which extend broadly up
inner orbit to a point $1.5 \times$ length of scape.

Frons impunctate, weakly microsculptured. Vertex transversely microsculptured. Ocelli closer to each other than to eyes. OOD $1.2\text{--}1.3 \times \text{LOD}$.

Mesosoma. Pronotal transverse carina foveolate laterally; transverse sulcus unsculptured; side irregularly carinate. Scutum and scutellum microsculptured. Scutum usually with a transverse row of microcarinae next to posterior margin; punctation variable, ranging from small sparse pinpricks to larger more dense (3–4 diameters apart) punctures more or less concentrated in the notaular region; anterior scutal margin nearly contiguously punctate between notaular grooves. Scutellum sparsely punctate on disc. Mesopleuron shiny, microsculpture at most weakly evident, nearly impunctate; scrobal sulcus absent; hypersternulus and omaulus weakly foveolate. Metapleuron impunctate, weakly microsculptured. Propodeal side shiny adjacent to metapleuron, otherwise microsculptured and finely areolate. Propodeal enclosure weakly defined, not carinate.

Metasoma. Weakly microsculptured. Punctures evanescent on terga I–III; posterior band of punctures on terga IV–VII that increases in width and puncture density towards posterior metasoma. Sterna minutely punctured.

Color. Ground color black. White to cream: palpi, mandibles except apically, antenna ventrally except apical flagellomeres, pronotal lobe, tegula, fore leg, mid leg except base of coxa and median area of femur, hind leg except base of coxa and basal $\frac{1}{5}$ of femur. Yellow-brown: apical flagellomeres of antenna, base of mid and hind coxae, median area of mid femur, basal $\frac{1}{5}$ of hind femur. Orange: apex of tergum VII of metasoma.

Female. Length 4–6 mm. Similar to male except as follows: clypeus without microsculpture, evenly punctured and setose, setae not obscuring underlying sculpture; punctures small about 1–2 diameters apart; apex with 2 median teeth separated by a shallow emargination; setae extend from

clypeus over subantennal area and up inner orbit to a point slightly greater than that of scapal apex. OOD $1.8\text{--}2.0 \times \text{LOD}$. Pygidial plate present, microsculptured, with several punctures. Antenna beyond pedicel brown; coxae, femora, and hind tibia suffused with brown; remaining area of legs more yellowed than in male. Apex of metasomal tergum VI orange.

Material Examined (26♂, 43♀).—**ARGENTINA: Neuquén:** Pucara, Lago Lacar. Pucara, P. Nac. Lanin. San Martin Andes. **CHILE: Arauco:** Contulmo, Palo Botado. **Aysen:** Lago Frio. Puerto Cisnes. **Cautín:** Afunahue Villarrica. **Chiloe:** Chiloe Island, Dalcahue. **Curico:** Cord. Curico, El Coigo. Cubillo, C. Curico. Estero La Juala, Los Quenes, Cord. Curico. **Los Lagos:** Corral (type locality). **Malleco:** P. N. Contulmo. Victoria, 4km s., 300m. **Nuble:** Las Trancas, Cord. Nuble (Chillan). **O'Higgins:** Graneros. **Santiago:** El Canelo. Lo Canas. **Talca:** Altos de Vilches, 1200m. **Valparaiso:** Los Andes. Vina del Mar. Valparaiso.

Distribution (Map 10).—Argentina, Chile.

2. *Araucastigmus masneri* Finnamore, new species

Derivation of Name.—The species is named in honour of Lubomir Masner, collector of half the known specimens.

Diagnosis.—Propodeum without shiny areas. Other species in the genus have a shiny area on the propodeum adjacent to the metapleuron.

Description.—Male. Length 4.0–5.5 mm.

Head. Flagellomeres without tyli. Head sparsely punctate, shiny, usually without microsculpture except on frons but larger specimens have evanescent microsculpture on vertex and gena. Clypeus and subantennal area obscured by dense appressed setae which extend up inner orbit to a point slightly greater than height of scape. Frons impunctate, microsculptured. Vertex minutely and sparsely punctate. Ocelli closer to each other than to eyes. OOD $1.8\text{--}1.9 \times \text{LOD}$.

Mesosoma. Pronotal transverse carina

foveolate laterally, transverse sulcus unsculpted; pronotal side with a few short carinae. Scutum with contiguous punctures between notaular grooves near anterior margin, otherwise impunctate or nearly so; shiny, without microsculpture; posterior margin weakly longitudinally microcarinate; notaular groove deeply impressed, foveolate. Scutellum shiny on anterior half, microsculptured on posterior half; with several scattered punctures on transverse midline. Mesopleuron shiny, without microsculpture, punctures sparse, obscure; scrobal sulcus absent. Hypersternaulus and omaulus foveolate. Metapleuron weakly microsculptured, impunctate. Propodeum without shiny areas, entirely microsculptured; evanescent, irregular, areolae on lateral spheres; propodeal enclosure not defined by a carina, with irregular carinae medially and on anterior margin.

Metasoma. Terga dull, microsculptured, punctures evanescent; posterior metasoma more shiny with punctures forming more or less discrete apical bands on terga. Sterna microsculptured, impunctate.

Color. Ground color black. White: palpi, mandible except apex, pronotal lobe, anterior spot on tegula. Brown to yellow-brown: scape, pedicel, at least flagellomeres I–V and occasionally I–XI, tegula except anterior spot, trochanters, fore and mid tibiae and tarsi, occasionally bases of sterna IV, V and apices of VI and VII.

Female. Length 4.5–5.5 mm. Similar to male except as follows: clypeus shiny, evenly punctured and setose, setae not obscuring underlying sculpture; punctures minute, 2–3 diameters apart. Clypeal apex with 2 teeth separated by shallow median emargination. Subantennal area less densely setose than clypeus. OOD $2.0\text{--}2.1 \times$ LOD. Scutum and mesopleuron more coarsely punctate than in male. Pygidial plate weakly microsculptured, with several punctures. Flagellum of antenna brown to black, mid tibia occasionally black, sterna black.

Material Examined (10♂, 20♀).—Holo-

type: ♂, CHILE: Cautín, Conguillio National Park, 1150m 4-II-1988 L. Masner, *Araucaria* [*Araucaria*?, *Araucariaceae*], *Nothofagus* [Fagaceae] (BRD). Paratypes: **ARGENTINA: Neuquén:** Lanín, Pucara 15-III-1971 Schajovskoy (♀: 4 IIES). **CHILE: Arauco:** Pichinahuel, Cord. Nahuelbuta 20-28-I-1959 L. Peña (♂: 1 BRD). **Aysen:** Lago Frio 20/23-I-61 L. Peña (♂: 1 MCZ). **Cautín:** same data as holotype (♂: 2 BRD, 2 PMA; ♀: 4 BRD, 5 PMA). **Los Lagos:** Osorno, Puyehue Nat. Pk., Antillanca, 1200m 16-II-1988 L. Masner, *Nothofagus* [Fagaceae] near treeline (♂: 1 BRD). **Magallanes:** Laguna Amarga, 12-60 Peña (♀: 1 IIES). Laguna Amarga, Natales XII-14-21-60 Luis Peña (♀: 1 OSU). **Malleco:** Cord. de las Raíces, 40km e. Curacautín 6-7-II-1979, 1200m D. & M. Davis & B. Akerbergs (♀: 1 USNM). Curacautín, R. Blanco II-64 Luis E. Peña (♂: 1 AEI). Icalma, 31-XII-1958 Luis E. Peña (♀: 1 BRD). Liucura 1800m, Jan. 1959 L.E. Peña (♀: 1 OSU). **Nuble:** Las Trancas 1600m 19-22-1979 (♀: 1 PMA). Las Trancas, Chillán I-19-22-1979, 1600m L. Peña (♀: 1 AEI). **O'Higgins:** Graneros 1100m 4-III-62 Peña (♀: 1 MCZ). **Valdivia:** 30km w. La Unión, Las Traucas 500m 8-11-II-1988 PT, L. Masner (♂: 1 BRD).

Distribution (Map 11).—Argentina: Neuquén. Chile.

3. *Araucastigmus yanillus* Finnamore, new species

Derivation of Name.—The name *yanillus* is derived from two Quechua terms, *yana* meaning black and *illay* meaning bright or shiny, in reference to the shiny black appearance of this species.

Diagnosis.—The extensive shiny areas in the female propodeum and in the male propodeum, the lack of sculpture overlying microsculpture, and the lateral shiny area next to the metapleuron will separate this species from all others in the genus. Other species have the propodeum entirely microsculptured or they have sculpture on at least lateral spheres.

Description.—Male. Length 4 mm.

Head. Flagellomeres without tyli. Head sparsely punctate, shiny, without microsculpture except sometimes evanescent microsculpture on gena. Clypeus and subantennal area obscured by dense appressed setae which extend up inner orbit to a point $1.1 \times$ length of scape. Lower frons impunctate, shiny; upper frons with several scattered punctures. Vertex sparsely punctate. Ocelli closer to each other than to eyes. OOD $1.5\text{--}1.6 \times$ LOD.

Mesosoma. Pronotal transverse carina foveolate laterally, several longitudinal carinae sometimes present near median region of transverse sulcus. Scutum with variable, non-contiguous punctures and a few fine, transverse microcarinae on anterior margin between notaular grooves; microsculpture present between admedian lines. Scutum otherwise shiny, without microsculpture, mostly impunctate, few punctures clustered posterior to notaular groove; notaular groove deeply impressed, foveolate; posterior margin of scutum smooth, without transverse row of longitudinal carinae. Scutellum shiny on anterior half, microsculptured on posterior half; a few punctures along transverse median discal area. Mesopleuron shiny, impunctate above sternopleural region; scrobal sulcus absent. Hypersternaulus foveolate; omaulus not foveolate, usually evanescent to absent toward hypersternaulus but continued ventrally. Metapleuron shiny, without microsculpture. Propodeum shiny laterally adjacent to metapleuron, otherwise microsculptured without raised lines (sculpture) except on median area of propodeal enclosure where several more or less transverse carinae are usually evident. Propodeal enclosure not defined by a carina.

Metasoma. Weakly microsculptured, somewhat shiny compared to other species; punctures minute, sparse, evanescent, not forming apical bands on posterior terga. Sterna microsculptured, impunctate.

Color. Ground color black. White: palpi, mandible except apically, pronotal lobe,

anterior spot on tegula, trochanters, fore and mid tarsi, coxae ventrally. Yellow-brown: scape, pedicel, flagellomeres I–VII ventrally, coxae dorsally, femora, tibiae, hind tarsus, and sterna beyond II more or less suffused.

Female. Length 4.5–5.5 mm. Similar to male except as follows: clypeus sparsely and evenly setose, more sparsely setose than in other species, punctures minute with several larger punctures medially. Clypeal apex with 2 teeth separated by shallow median emargination. Subantennal area without setae. OOD $2.1 \times$ LOD. Propodeum with sculpture on lateral spheres variable from nearly completely shiny (most specimens) to almost entirely microsculptured, without sculpture overlying microsculpture; area adjacent to metapleuron shiny. Pygidial plate narrow with median area minutely punctate. Mid and hind legs brown except trochanters.

Material Examined (8♂, 10♀).—Holotype: ♀, CHILE: Cautín: Conguillio National Park 1150m 4-II-1988 L. Masner, *Araucaria* [*Araucaria*?, *Araucariaceae*], *Nothofagus* [*Fagaceae*] (BRD). Paratypes: **ARGENTINA: Neuquén:** Pucara (S.M. Andes) XII-6-16-1968 C.C. Porter (♂: 1 MCZ). **CHILE: Arauco:** Pichinahuel, Cord. Nahuelbuta 10-20-I-1959 L. Peña (♀: 1 BRD). **Cautín:** same data as holotype (♂: 5 BRD, 2 PMA; ♀: 1 BRD, 5 PMA). **Curico:** El Coigo Jan-1961 J. Foerster (♀: 1 BRD). **Nuble:** Las Trancas, 1400m Chillan XII-19-21-1983 Luis Peña (♀: 1 AEI).

Distribution (Map 12).—Argentina: Neuquén. Chile.

PARACRABRO Turner (Figs. 16, 17)

Paracrabro Turner 1907:274. Type species: *Paracrabro froggatti* Turner, 1907 by original designation and monotypy.

Diagnosis.—The presence of an acetabular carina, hind wing media diverging just before cu-a, and the lack of a discrete micropore field on the vertex will separate this genus from all others in the Stigmina.

Description.—Head. Labrum weakly quadrilobed (appears bilobed), median lobes evanescent. Mandible with apex bidentate in male, pentadentate in female; apicoventral tooth in female acute; inner basal tooth absent. Clypeal apex in male without bevelled modifications; female clypeus with 4 apical teeth although median teeth are greatly reduced imparting a bidentate appearance. Interantennal tubercle present, protruding. Frontal carina present as a simple raised line immediately above interantennal tubercle. Vertex with loose association of pits rather than micropore field; pits shifted anteriorly in female. Inner orbits parallel in female, converging below in male. Eye margined by a carina on inner orbit in female, entirely margined in male. Occipital carina foveolate, more or less raised ventrally, not intersecting hypostomal carina.

Mesosoma. Scutum without median groove, notaular groove not elongate. Acetabular carina present, omaulus intersecting acetabular carina, subomaulus absent. Scrobal sulcus absent in female, evanescent in male. Hypoepimeral area without coarse sculpture except in area of scrobal sulcus in male, microsculptured only. Mid basitarsus of male flattened, curved with posterior subapical expansion. Hind tibia excluding apex, with 4 posterior spines in female, 2 in male. Fore wing cellular area without setae in male, setae present in female. Hind wing media diverging at cu-a; hind wing submedian cell not reduced, of normal size.

Metasoma. Petiole rounded, carinae present apically and basally. Pygidial plate narrow, trough-like, absent in male. Male genitalia unusually elongate relative to other genera in the subtribe, digitus elongate relative to cuspis.

Distribution (Map 13).—Australia.

Paracrabro froggatti Turner

Paracrabro froggatti Turner 1907:275 ♀. Holotype ♀ (not examined), Australia: Victoria.

Description.—See generic description above.

Material Examined (1♂, 1♀).—**AUSTRALIA: New South Wales:** Elizabeth Beach, 21km s. Forster. **Western Australia:** Gascoyne Exp. Sta., Carnarvon.

Distribution (Map 13).—Australia.

AYKHUSTIGMUS Finnermore, new genus (Figs. 18–29)

Derivation of Name.—Aykhu is a Quechua term meaning extravagant or fancy in reference to the unusually complex sculpturing found in members of this genus.

Diagnosis.—The coarsely sculptured mesopleuron will separate this genus from all others in the Stigmina.

Description.—Head. Labrum quadrilobed, with a shallow broad median emargination. Mandible with apex in male bidentate, in female tridentate; apicoventral tooth in female acute; inner basal tooth absent. Clypeal apex in male without bevelled modification; female clypeal apex with 4 teeth. Interantennal tubercle absent. Frontal carina absent. Vertex with micropore field between lateral ocellus and eye margin. Inner orbits converging below. Eye margined by a strong carina. Occipital carina present, complete, not joining hypostomal carina, simple in female, raised and foveolate in male.

Mesosoma. Scutum with median groove usually absent but occasionally evanescent posteriorly; notaular groove normal, not elongate. Acetabular carina present, intercepted by omaulus. Scrobal sulcus present, evanescent. Hypoepimeral area coarsely sculptured. Mid basitarsus in male unmodified. Posterior margin of hind tibia with 2 or 3 spines. Fore wing with setae absent from cellular area. Hind wing with media diverging before or after cu-a; submedian cell of normal size, not reduced.

Metasoma. Petiole carinate. Pygidial

plate narrow, absent in male. Genitalia with digitus elongate, acute, cuspis (lobed?) with tooth.

Type Species.—*Aykhustigmus patanawi* new species.

Distribution (Map 36).—Neotropical, south of the Brazilian Highlands although a single record exists for Venezuela, possibly an introduced species or mislabelled specimen.

KEY TO SPECIES OF *AYKHUSTIGMUS*

(Male of *A. phasti* is unknown)

- | | |
|--|---|
| 1 Males | 2 |
| 1' Females | 4 |
| 2 Hind wing media diverging before cu-a (Fig. 48); vertex and gena striatopunctate (Figs. 19, 21); frons irregularly carinate; scutum closely and coarsely punctate to striatopunctate posteriorly (Fig. 23) | 2. <i>patanawi</i> Finnamore, new species |
| 2' Hind wing media diverging after cu-a (Fig. 49); head at most with microsculpture; scutum with smaller more widely separated punctures | 3 |
| 3 Frons with pair of small swellings anterior to mid ocellus on each side of frontal carina | 1. <i>fritzi</i> Finnamore, new species |
| 3' Frons smoothly rounded, without swellings | 4. <i>warawa</i> Finnamore, new species |
| 4 Hind wing media diverging before cu-a (Fig. 48); vertex transversely striatopunctate; upper frons striatopunctate | 2. <i>patanawi</i> Finnamore, new species |
| 4' Hind wing media diverging after cu-a (Fig. 49); frons and vertex at most with microsculpture | 5 |
| 5 Frons with a pair of broad swellings anterior to mid ocellus that are visible in lateral profile | 1. <i>fritzi</i> Finnamore, new species |
| 5' Frons evenly rounded, without swellings | 6 |
| 6 Clypeus with 4 apical teeth (Fig. 24); scutum microsculptured on anterior ¼ to ½, shiny and punctate to striatopunctate on posterior half (Fig. 29) | 4. <i>warawa</i> Finnamore, new species |
| 6' Clypeus with 2 apical teeth; scutum shiny, without microsculpture, carinate on median third | 3. <i>phasti</i> Finnamore, new species |

1. *Aykhustigmus fritzi* Finnamore, new species

Derivation of Name.—The species is named in honour of Manfredo A. Fritz, collector of most of the specimens I have seen of the genus.

Diagnosis.—The hind wing media diverging after cu-a, swellings on the upper frons, and microsculpture on the anterior scutum will distinguish this species from all others in the genus.

Description.—Male. Length 4 mm.

Head. Flagellomeres without tyli. Clypeus and subantennal area obscured by dense appressed setae that extend up inner orbits to a point about ¾ length of scape. Eye margined by a coarse carina

that is interrupted ventrally near base of mandible. Carina foveolate, except on vertex and separated from outer orbit by a distance subequal to basal width of mandible. Frons microsculptured and impunctate on lower face; shiny, with evanescent microsculpture on upper surface to lateral ocellus where it is sparsely punctate with punctures at least 3 diameters apart. Upper frons with a swelling on each side of frontal line that is just visible in lateral profile. Vertex microsculptured, with a circular depression on midline posterior to lateral ocelli. Posterior vertex with an evanescent transverse ridge (posterior to circular depression) connecting outer orbital carinae. Ocelli closer to each other than to

eyes. OOD $1.8 \times$ LOD. Gena microsculptured, punctures evanescent; irregular evanescent carinae radiate from occipital carina on lower genal area. Occipital carina considerably raised, coarsely foveolate to mid ventral line.

Mesosoma. Pronotum with transverse carina greatly raised, toothed at lateral end; carina continued on side to antero-ventral corner which is produced anteriorly as a tooth that surpasses dorsolateral tooth in size. Pronotum with transverse sulcus longitudinally carinate; setae sparse, not obscuring sculpture. Pronotal side longitudinally carinate. Scutum microsculptured anteriorly, shiny evanescent microsculpture posteriorly. Scutum between notaular grooves, striatopunctate, elsewhere sparsely punctate. Scutellum shiny anteriorly, microsculptured posteriorly, with a foveolate transverse sulcus on lateral disc. Mesopleuron coarsely areolate from subalar fossa to sternopleural region. Scrobal sulcus indicated by slight depression. Hypersternaulus and omaulus coarsely foveolate. Mesosternum microsculptured, punctate next to areas of areolate sculpture on sternopleural region. Metapleuron microsculpture evanescent with a few irregular longitudinal carinae. Hind wing media diverging after cu-a. Propodeum coarsely areolate, except area next to metapleuron which is weakly carinate.

Metasoma. Terga shiny, without microsculpture, impunctate. Sterna shiny, without microsculpture, with several punctures on lateral margins.

Color. Ground color black. White: pronotal lobe. Yellow-brown: palpi, mandible except apex, antenna, tegula, wing veins, stigma, legs.

Female. Length 3.5 mm. Similar to male except as follows: clypeus with 2 median teeth separated by a deep semicircular emargination; setose, although less so than male; setae partially obscuring densely punctate surface. Subantennal area and inner orbits sparsely setose. Inner

orbits margined by an evanescent, non-foveolate carina. Eye elsewhere not margined by carina. Frons between swellings and lateral ocelli, shiny, weakly microsculptured with coarse sparse punctures (3 or more diameters apart). Vertex without circular depression or transverse ridge but with frontal line continued as a sulcus on midline posterior to ocelli. OOD $1.7 \times$ LOD. Gena with coarse sparse punctures. Occipital carina simple, not raised or foveolate. Pronotum with teeth less prominent than in male. Metasomal terga and sterna shiny with sparse punctures; sternum VI densely punctate. Pygidial plate narrow, shiny, bisected by a longitudinal ridge, with several coarse punctures.

Material Examined (1♂, 2♀).—Holotype: ♂, PARAGUAY: S. Bernardino, Mitte Decbr., Fiebrig (NMW). Paratypes: **BOLIVIA:** Km 335 de Cochabamba a Santa Cruz, Fritz -Martinez Col. (♀: 1 IIES). **BRAZIL: Estado do Ceara:** Ceara, Baturite 17-6-1908, Ducke (♀: 1 MPEG).

Distribution (Map 14).—Brazil: Ceara. Bolivia, Paraguay.

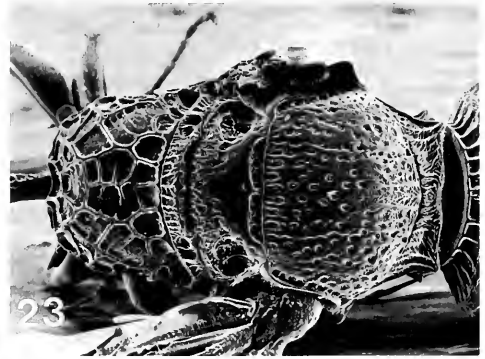
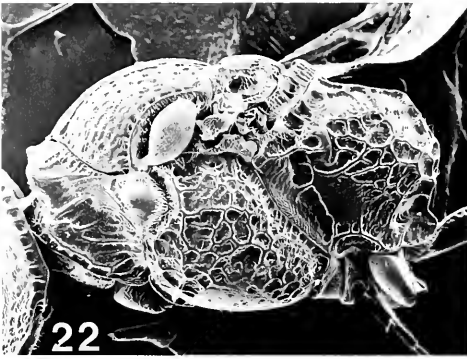
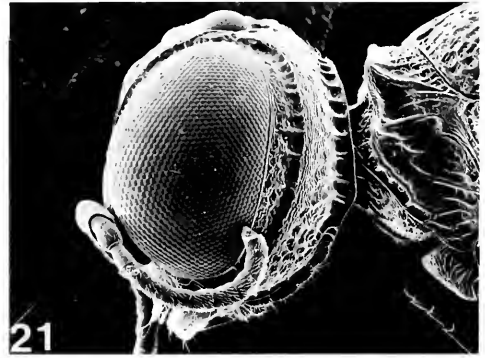
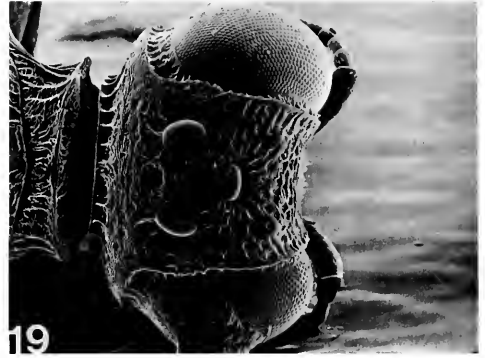
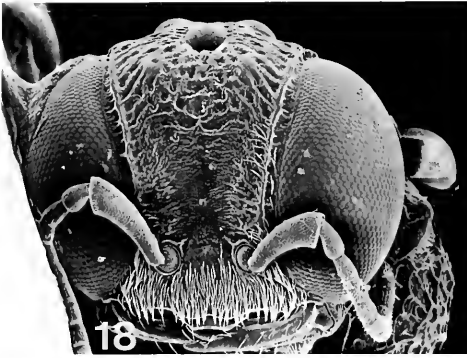
2. *Aykhustigmus patanawi* Finnamore, new species

Derivation of Name.—The species epithet is derived from two Quechua terms, "pata" meaning margin and "nawi" meaning eye, in reference to the margined eye of this species.

Diagnosis.—Hind wing media diverging before cu-a and vertex with transverse carinate sculpture.

Description.—Male. Length 4.2 mm.

Head. Flagellomeres without tyli. Clypeus and subantennal area obscured by dense appressed setae that extend narrowly up inner orbit to a point about $1\frac{1}{2}$ height of scape. Eye margined by a coarse foveolate carina that is interrupted ventrally at base of mandible. Carina separated from mid point of outer orbit by a distance subequal to basal width of mandible. Frons with frontal surface impunctate, microsculptured; irregular transverse ca-



Figs. 18–23. *Aykhustigmus patanawi* ♂. 18, head, frontal view. 19, head and prothorax, dorsal view. 20, micropore field between lateral ocellus and compound eye. 21, head, lateral view. 22, mesosoma, lateral view. 23, mesosoma, dorsal view.

rinae laterally next to inner orbital carina. Upper frons with coarse more or less irregular striatopunctate sculpture radiating from mid ocellus, punctures less than 1 diameter apart; small swelling on either side of mid line just anterior to mid ocellus. Vertex densely microsculptured with large, median, circular depression poste-

rior to lateral ocelli; several short carinae radiating from lateral ocellus. Posterior vertex with a series of 3 or 4 transverse, striatopunctate ridges extending between outer orbits posterior to orbital carinae. OOD $0.9\text{--}1.3 \times \text{LOD}$. Gena entirely carinate or lower area areolate, sculpture in either case continuous from occipital ca-

rina to hypostomal carina and outer orbital margin. Occipital carina considerably raised, lamella-like, coarsely foveolate to mid ventral line.

Mesosoma. Pronotum with transverse carina considerably raised, toothed at lateral end; carina continued ventrally on propodeal side to anteroventral corner which is produced anteriorly as tooth subequal in size to dorsolateral tooth. Pronotum with transverse sulcus longitudinally carinate; setae sparse, not obscuring sculpture. Pronotal side with irregular longitudinal carinae. Scutum microsculptured anteriorly and in depressions medially and posteriorly; striatopunctate, punctures coarse, variable from relatively sparse, about 1 diameter apart on disc to nearly contiguous; notaular groove deeply impressed, foveolate, continued over half length of scutum. Scutellum microsculptured, with foveolate transverse sulcus on mid lateral disc. Mesopleuron coarsely areolate from subalar fossa to sternopleural region. Scrobal sulcus indicated by slight depression. Hypersternaulus and omaulus coarsely foveolate. Mesosternum microsculptured, sparsely punctate. Hind wing media diverging before cu-a. Metapleuron microsculptured, few short carinae on posterior margin. Propodeum microsculptured and coarsely areolate, except for side next to metapleuron which is without areolae and partially without microsculpture.

Metasoma. Terga shiny with slight oily sheen, appearing impunctate on anterior terga (punctures minute, sparse, evanescent) but punctures increasing in size and density on posterior terga. Sterna shiny with slight oily sheen, punctures sparse throughout.

Color. Ground color back. White: pronotal lobe. Yellow-brown to brown: palpi, mandible except apex, antenna, legs, tegula, wing veins, stigma.

Female. Length 4.5 mm. Similar to male except as follows: clypeus with 2 median teeth separated by a deep semicircular

notch; setae dense, obscuring underlying sculpture. Setae less dense on subantennal area and inner orbit. Inner orbit margined by a non-foveolate carina that extends to vertex. Outer orbit without carina. Frons with lower area impunctate, densely microsculptured; upper area with evanescent microsculpture, shiny, obscurely striatopunctate; carinae, if present, radiating from mid ocellus anteriorly. Frons with small swelling on either side of mid line. Vertex with reduced circular depression posterior to ocelli (not evident in 1 specimen). Vertex densely microsculptured, with a series of irregular, transverse fine carinae between and posterior to outer orbits. Gena carinate and punctate near mandible, elsewhere microsculptured. OOD $1.9\text{--}2.1 \times \text{LOD}$. Occipital carina simple, complete, not raised or foveolate. Punctuation of metasoma as in male except sternum VI densely punctate. Pygidial plate narrow, shiny, bearing a lateral row of punctures.

Material Examined (1♂, 3♀).—Holotype: ♂, ARGENTINA: B. Aires, La Plata (Fac. Agronomia) X-XI-68 C. Porter (MCZ). Paratypes: ARGENTINA : Buenos Aires: Moreno, Fritz (♀: 1 IIES). Moreno, 12-73 Fritz (♀: 1 IIES). Tigre XI-39 Viana Leg. (♀: 1 IIES).

Distribution Map 15.—Argentina: Buenos Aires.

3. *Aykhustigmus phasti* Finnamore, new species

Derivation of Name.—Phasti is a Quechua term meaning naked or bare in reference to the lack of microsculpture on the scutum and the resulting naked appearance.

Diagnosis.—Male unknown. Female: the absence of microsculpture on the scutum will distinguish this species from others in the genus. In addition the hind wing media diverges after cu-a, the vertex is without a transverse carinae, and the clypeal apex has 2 teeth.

Description.—Female. Length 4 mm.

Head. Clypeus with 2 teeth on apical margin separated by a deep U-shaped notch; surface partially obscured by dense appressed setae which extend up subantennal area and narrowly up inner orbit to about $\frac{3}{4}$ height of scape. Inner orbit with non-foveolate carina that is evanescent toward vertex. Outer orbit not margined. Frons microsculptured on scapal basin, impunctate; upper frons more or less shiny with evanescent microsculpture, punctures sparse. Vertex sometimes with poorly defined depression posterior to lateral ocelli on mid line or depression absent; densely microsculptured in contrast to upper frons. OOD 1.8–1.9 \times LOD. Gena microsculptured, punctate toward mandibular base. Occipital carina simple, complete, not raised or foveolate.

Mesosoma. Pronotum with transverse carina considerably raised, lateral end forming right angle that continues ventrally on carinate pronotal side to anteroventral corner which is produced as a small tooth. Pronotum with transverse sulcus longitudinally carinate. Scutum shiny, without microsculpture except weakly at extreme anterolateral corner, median third (between notaular grooves) striatopunctate; lateral area punctate, usually more densely punctate next to notaular groove. Scutellum shiny or weakly microsculptured anteriorly, microsculptured posteriorly; a foveolate, transverse sulcus on mid lateral disc; punctures few, present on anterolateral disc. Mesopleuron coarsely areolate from subalar fossa to sternopleural region. Scrobal sulcus indicated by a slight depression. Hypersternaulus and omaulus coarsely foveolate. Mesosternum microsculptured, sparsely punctate. Metapleuron weakly microsculptured, a few short carinae on posterior margin. Hind wing media diverging after cu-a. Propodeum with microsculpture evanescent or absent over most of its surface; coarsely areolate, except next to metapleuron which is irregularly carinate.

Metasoma. Terga shiny; punctures

sparse, evanescent on anterior terga, more apparent on posterior terga. Pygidial plate with slight raised median basal ridge. Sterna shiny, sparsely punctate except sternum VI which is densely punctate.

Color. Ground color black. White: mandible on basal third, pronotal lobe. Yellow-brown to brown: palpi, mandible except apex and basal third, antenna, legs, tegula, wing veins, stigma.

Material Examined (3♀).—Holotype: ♀, ARGENTINA: San Isidro I-1976 B.A. (PMA). Paratypes: ARGENTINA : **Entre Ríos**: Palmar Colon I-74 Fritz (♀: 1 IIES). VENEZUELA : **Zulia**: 6km w. La concepcion, 18-VI-1976 A.S. Menke & D. Vincent (♀: 1 USNM).

Distribution (Map 16).—Argentina, Venezuela. The Venezuelan record represents the only collection locality north of the Brazilian Highlands for the genus and could represent an introduction of this species to that area.

4. *Aykhustigmus warawa* Finnamore, new species

Derivation of Name.—The species epithet, warawa, is a Quechua term meaning adorned in reference to the elaborate sculpture of this species.

Diagnosis.—The combination of the hind wing media diverging after cu-a; and frons without swellings, smoothly rounded in both sexes; and the female clypeal edge with 4 teeth, and scutum microsculptured on anterior $\frac{1}{4}$ or more will separate this species from all others in the genus.

Description.—Male. Length 3.0–4.5 mm.

Head. Flagellomeres without tyli. Clypeus and subantennal area obscured by dense appressed setae that extend up inner orbit about $1\frac{1}{4}$ length of scape. Inner orbit margined by non-foveolate carina extending $\frac{2}{3}$ up frons. Outer orbit margined from base of mandible to vertex by foveolate carina or evanescent non-foveolate ridge in smaller specimens; at mid point the carina is separated from orbit by distance subequal to basal width of man-

dible. Lower frons microsculptured; upper frons shiny, weakly microsculptured, punctate. Vertex microsculptured with puncture-like depression on mid line posterior to lateral ocelli; transverse evanescent ridge connects laterally with outer orbital carina. Lateral ocelli closer to each other than to eye. OOD $1.3\text{--}1.4 \times \text{LOD}$. Gena microsculptured, punctate near base of mandible. Occipital carina complete, foveolate, not raised.

Mesosoma. Pronotum with transverse carina raised, lateral end with small tooth; carina continued on pronotal side to anteroventral corner which is produced as tooth surpassing in size that of dorsolateral tooth. Pronotum with transverse sulcus longitudinally carinate; setae sparse, not obscuring sculpture. Pronotal side with irregular, longitudinal carinae. Scutum with microsculpture variable from densely microsculptured to microsculptured on anterior margin only; punctures present on median third (between notaular grooves which extend posteriorly as somewhat polished low ridges); lateral areas impunctate to sparsely punctate; posterior margin and often median area striatopunctate. Scutellum shiny, weakly microsculptured anteriorly, punctured; posterior microsculptured, impunctate; without foveolate sulcus on disc laterally. Mesopleuron coarsely areolate from subalar fossa to sternopleural region. Scrobal sulcus indicated by slight depression. Hypersternaulus and omaulus coarsely foveolate. Mesosternum microsculptured, sparsely punctate. Metapleuron shiny, without or with evanescent microsculpture, several short carinae on posterior margin. Hind wing media diverging after cu-a. Propodeum microsculptured, coarsely areolate, except for side next to metapleuron which is shiny, unsculptured.

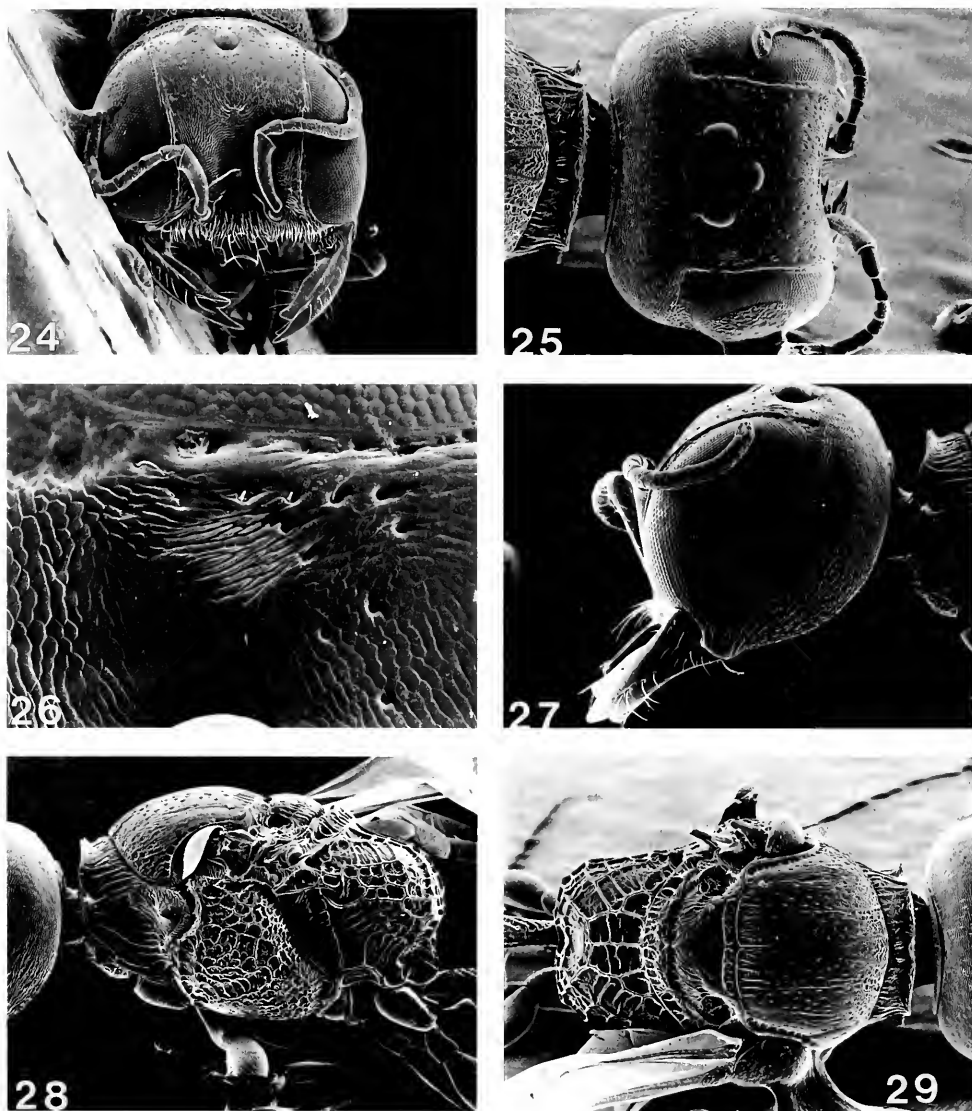
Metasoma. Terga shiny with slight oily sheen, punctures sparse and evanescent. Sterna similar to terga except punctures more dense.

Color. Ground color black. White: pronotal lobe. Yellow-brown to brown: palpi, mandibles except apically, antenna, legs, tegula, wing veins, stigma.

Female. Length 4.0–4.5 mm. Similar to male except as follows: clypeus with 4 teeth on apical margin, lateral teeth located below inner antennal socket margin and often obscured by overhanging clypeal setae. Surface of clypeus and subantennal area obscured by dense appressed setae which extend up inner orbit $3/4$ length of scape. Outer orbit unmarginated. Lower gena striatopunctate. OOD $1.4\text{--}1.6 \times \text{LOD}$. Occipital carina simple, complete, not raised or foveolate. Pygidial plate narrow, shiny, sparsely punctate. Sternum VI densely punctate.

Material Examined (13♂, 13♀).—Holotype: ♂, ARG. [ARGENTINA]: Salta: Rosario [de] Lerma 10–84 Fritz (IIES). Paratypes: **ARGENTINA: Buenos Aires:** 48–889 (♀: 1 MACN). Burzaco Sea L. 12–13-III-1974 C.R. Vardy B.M. 1974–204 (♀: 1 BMNH). Moreno, M.A. Fritz (♂: 1 IIES). Moreno 1–73, Fritz (♀: 2 IIES). La Plata (Fac. Agronomia) X-XI-68, C. Porter (♂: 1 MCZ). **Jujuy:** Palpala II-1968, M. Aczel (♀: 1 TMA). **Salta:** Pecitos 12–56, Fritz (♂: 1 IIES). Rosario [de] Lerma 10–84, Fritz (♂: 4 IIES). Urundel 26-I-950, R. Golbach (♀: 1 LILLO). Santiago del Estro: Baez 2–74, Martinez (♀: 1 IIES). **Tucuman:** Las Higueras XI-57, Ogloblin (♂: 1 IIES). San Janvier 21-X-1950, M. Aczel (♂: 1 LILLO). San Miguel, Tucuman 18-XI-1979, L.A. Stange (♂: 1 FSCA). San Pedro de Colalao, Foerster (♀: 1 IIES). Trancas, Fritz (♂: 1 IIES, ♀: 1 IIES). **BOLIVIA: Beni:** Ichilo Yapacani 2–71, Fritz (♂: 1 IIES, ♀: 1 IIES). **BRAZIL: Santa Catarina:** Nova Teutonia Feb. 1957, F. Plaumann (♀: 2 OSU). **Sao Paulo:** Campinas Mar. 1924, F.X. Williams (♂: 1 BISH). Unplaced: Minas, Jacare Dec. 1–1907 Carn. Mus. Acc. 3533 (♀: 1 CARN).

Distribution (Map 17).—Argentina, Bolivia, southern Brazil.



Figs. 24-29. *Aykhustigmus warawa* ♀. 24, head, frontal view. 25, head and prothorax, dorsal view. 26, micropore field between lateral ocellus and compound eye. 27, head, lateral view. 28, mesosoma, lateral view. 29, mesosoma, dorsal view.

INCASTIGMUS Finnamore, new genus
(Figs. 30-35)

Derivation of Name.—*Incastigmus* is named after the indigenous Inca people of South America.

Diagnosis.—The presence of a median groove or posteromedian pit on the scutum will separate this genus from all others in the Stigmina.

Description.—Head. Labrum quadri-lobed with narrow, deep median emargination. Mandible with apex in both sexes tridentate; apicoventral tooth in female acute; inner basal tooth absent. Clypeal apex in male without bevelled modifications; with 4 teeth in female. Interantennal tubercle absent. Frontal line absent. Micropore field present. Inner orbits converging

below. Eye at most partially margined by a carina. Occipital carina complete, not joining hypostomal carina, simple in female; raised, foveolate in male.

Mesosoma. Scutum with a median groove or at least a posteromedian pit; notaular groove usually elongate. Acetabular carina intercepting omaulus. Scrobal sulcus present. Hypoepimeral area without coarse sculpture. Mid basitarsus of male elongate, as long as next 3 tarsomeres combined. Posterior margin of hind tibia with 2 or 3 spines. Fore wing without setae in cellular area. Hind wing media diverging before cu-a; submedian cell of normal size, not reduced.

Metasoma. Petiole carinate. Pygidial plate narrow, absent in male. Digitus elongate relative to cuspis, clubbed.

Type Species.—*Incastigmus inti* new species.

Distribution.—Neotropical.

Species Transferred.—*Stigmus hexagonalis* Fox, *S. neotropicus* Kohl, *S. smithii* Ashmead, and *S. thoracicus* Ashmead. The 25 species of *Incastigmus* are the subject of the forthcoming Part 2 of this revision.

Incastigmus inti Finnamore, new species

Derivation of Name.—Inti is a Quechua term meaning sun in reference to the central position of this species as type for the genus.

Diagnosis.—The combination of the following characters will separate this species from all others in the genus. Micropore field on vertex oval. Scutum with median and notaular grooves complete from anterior to posterior margin, without regular longitudinal carinae between grooves. Pronotal lobe white, rounded conical, not flattened or toothed or dark. Male antenna with tylus on apical flagellomere. Female clypeus with 2 elongate setae issuing from 2 narrowly separated pits on median lobe. Female frons shiny, without microsculpture anterolaterally to mid ocellus.

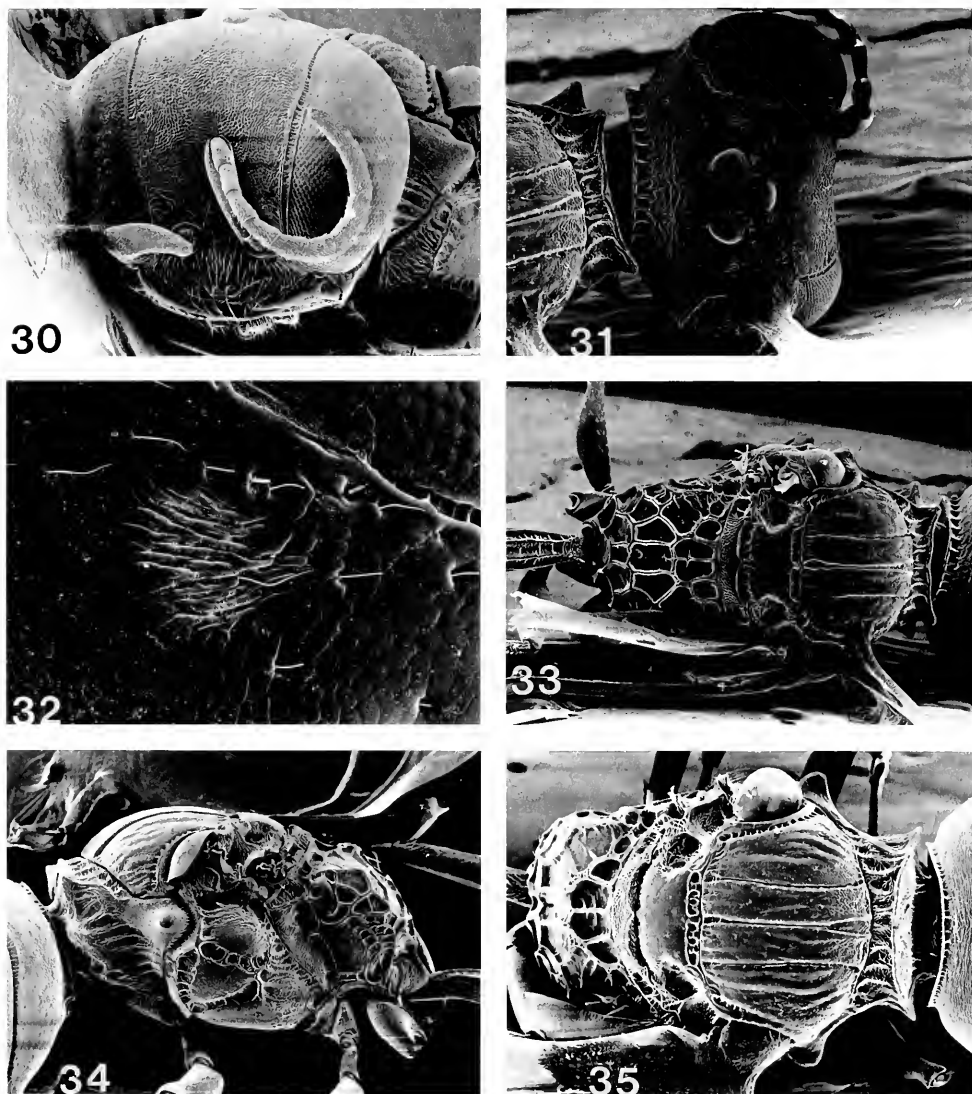
Description.—Male. Length 2.5–4.0 mm.

Head. Flagellomeres without specialized setae; II–XI with tyli, that on flagellomere XI imparting asymmetrical shape; basal flagellomere length $2.2 \times$ apical width; penultimate flagellomere length $1.4 \times$ apical width. Head microsculptured on lower frons, mid frons and vertex but shiny on upper lateral frons, punctures sparse. Clypeus obscured by dense appressed setae which extend up inner orbits little more than height of antennal socket. Micropore field present as discrete patch. Ocelli closer to each other than to compound eyes. OOD $1.7 \times$ LOD. Gena microsculptured, sparsely punctate, non-carinate, without ventral tooth or swelling. Occipital carina foveolate.

Mesosoma. Transverse carina of pronotum toothed laterally, continued ventrally to pronotal side and terminating in a ventrolateral tooth; transverse sulcus longitudinally carinate. Pronotal side carinate, lobe conical with rounded apex. Scutum entirely microsculptured to weakly microsculptured with shiny patches; notaular groove complete to posterior margin; median groove complete to anterior margin; punctures sparse. Scutellum microsculptured. Mesopleuron variable from entirely microsculptured to weakly shiny with reduced microsculpture, sparsely punctate to impunctate. Preomaular area with sparse setae that do not obscure underlying sculpture. Hypersternaulus, omaulus and scrobal sulcus foveolate. Metapleuron usually microsculptured. Propodeum shiny, generally without microsculpture, uniformly coarsely areolate except anterolaterally without sculpture.

Metasoma. Terga shiny, microsculpture and punctures evanescent (appearing impunctate). Sterna weakly microsculptured, punctures sparse.

Color. Ground color black. White: mandible medially, pronotal lobe. Yellow-brown: palpi, mandible subapically, antenna, fore leg except coxa, mid leg except coxae, hind trochanter and tarsus, tegula, metasomal sternum VIII.



Figs. 30–35. *Incastigmus inti*. 30, ♀ head, frontal view. 31, ♂ head and prothorax, dorsal view. 32, ♂ micropore field between lateral ocellus and compound eye. 33, ♂ mesosoma, dorsal view. 34, ♀ mesosoma, lateral view. 35, ♀ mesosoma, dorsal view.

Female. Length 3.0–4.25 mm. Similar to male except as follows: antenna without tyli, penultimate flagellomere length $1.25 \times$ apical width. Clypeus shiny, usually sparsely punctate, occasionally moderately dense punctation grouped in median area; median lobe with 2 elongate setae issuing from 2 narrowly separated pits; apex with truncate median lobe. Scutum with several irregular carinae between no-

taular and median grooves. Color as above but variable to dark antennal flagellum and dark femora.

Material Examined (258♂ 109♀).—Holotype: ♂, ECUADOR: Napo Prov. Tena, sweep 15-II-1986 A.T. Finnamore (PMA). Paratypes: **BOLIVIA: La Paz:** Chulumani 1,700m 25-III-1979 M. Cooper B.M. 1979–216 (♀: 2 BMNH). Chulumani 1,700m 30-III-1979 M. Cooper B.M. 1979–216 (♀: 1

BMNH). Chulumani 1,700m 31-III-1979 M. Cooper B.M. 1979-216 (♂: 1 BMNH). Chulumani 1,700m 3-IV-1979 M. Cooper B.M. 1979-216 (♂: 1 BMNH. ♀: 2 BMNH). Coroico-Chulomani III-7-1968 Garcia & Porter (♀: 1 MCZ). Coroico, Sta. Barbara 1100m 4-I-1975 (♀: 1 PMA). Tumupasa Dec. W.M. Mann, Mulford Biol. Expd. 1921-1922 (♂: 1 USNM). Yungas, 13km s. Caranavi 850m 27-III-1973 J. Helava (♀: 2 PMA). Unplaced: Las Juntas Dec. 1913, Steinbach (♀: 1 CARN). **BRAZIL: Mato Grosso:** Itaum III-1974 M. Alvarenga (♀: 3 AEI). **Para:** Belem IPEAN XII-1-4-1969 J.M. & B.A. Campbell (♀: 1 BRD). **COLOMBIA: Caqueta:** Florencia 480m 31-X-1971 M. Cooper B.M. 1972-275 (♀: 1 BMNH). Yuruyaco, 73k sw. Florencia 3-II-1979 M. Cooper B.M. 1979-106 (♀: 1 BMNH). Yuruyaco, 73k sw. Florencia 12-II-1979 M. Cooper B.M. 1979-106 (♂: 1 BMNH). Yuruyaco, 73k sw. Florencia 13-II-1979 M. Cooper B.M. 1979-106 (♂: 1 BMNH). **Putumayo:** Mocoa 13-IV-1974 M. Cooper B.M. 1974-327 (♂: 1 BMNH). Mocoa 16-IV-1974 M. Cooper B.M. 1974-327 (♀: 5 BMNH). Mocoa 18-IV-1974 M. Cooper B.M. 1974-327 (♂: 1 BMNH). Mocoa 19-IV-1974 M. Cooper B.M. 1974-327 (♂: 1 BMNH). Mocoa 14-VI-1974 M. Cooper B.M. 1974-548 (♂: 1 BMNH). Mocoa 24-VI-1974 M. Cooper B.M. 1974-548 (♂: 2 BMNH). Mocoa 26-VI-1974 M. Cooper B.M. 1974-548 (♀: 2 BMNH). Mocoa 16-VII-1978 M. Cooper B.M. 1978-431 (♀: 1 BMNH). Mocoa 7-IX-1974 M. Cooper B.M. 1975-33 (♂: 1 BMNH). Mocoa 27-IX-1974 M. Cooper B.M. 1975-33 (♂: 1 BMNH). Mocoa 600m 26-III-1976 M. Cooper B.M. 1976-290 (♂: 1 BMNH). Mocoa 18-III-1978 M. Cooper B.M. 1978-431 (♂: 1 BMNH). Villa Garzon, 8 mi s. Mocoa 3-VIII-1978 M. Cooper B.M. 1978-431 (♂: 1 BMNH). **Vaupés:** Mitu 11-V-1974 M. Cooper B.M. 1974-327 (♂: 1 BMNH). **ECUADOR: Carchi:** Chical 1250m 0-56N 78-11W, 1-VIII-1983 J. Rawlings, M. Smyers (♀: 1 CARN). **Napo:** Coca, May 1965 Luis Peña (♂: 1 AEI). Coca & Napo Rivers, V-1-12-65,

Luis Peña (♂: 1 AEI). Limoncocha 250m, 15-28-VI-1976 S. & J. Peck (♂: 2 BRD, ♀: 2 BRD). Misahualli, down Río Napo 19-II-1983 L. Huggert (♂: 15 PMA, ♀: 2 PMA). Muyuna, 5km w. Tena 29-IX-1978 M. Cooper B.M. 1979-20 (♀: 1 BMNH). Puerto Misahualli 350m II-1983 Sharkey (♂: 2 PMA, ♀: 3 PMA). Puerto Misahualli, 30km e. 350m II-1983 Sharkey (♂: 9 PMA). Santa Cecilia III-25-31-1969 P. & P. Spangler (♂: 1 USNM). Tena 9-14-II-1971 M. Cooper B.M. 1972-275 (♂: 1 BMNH). Tena 8-VII-1976 S. & J. Peck (♀: 3 PMA). Tena 400m II-1983 M. Sharkey (♂: 6 PMA, ♀: 1 PMA). Tena, sweep 15-II-1986 A.T. Finnermore (♂: 12 PMA, ♀: 3 PMA). Tena, sweep 18-II-1986 A.T. Finnermore (♀: 1 PMA). Tena, 12km sw. 500m 8-11-VII-1976 S. & J. Peck (♀: 1 BRD). Tena-Puyo Hwy. 5km n. Santa Clara 21-II-1986 sweep, T. Thormin & J. Wojcicki (♂: 1 PMA). **Pastaza:** Puyo 960m 1-8-X-1970 J. & M. Sedlacek (♂: 8 BISH). Puyo 900-960m 1-8-X-1970 J. & M. Sedlacek (♂: 7 BISH). Puyo 22km sw. 900m 14-16-VII-1976 S. & J. Peck, forest (♂: 1 BRD, ♀: 2 BRD). Puyo 23km se 19-V-1977 P.J. Spangler & D.R. Givens #58 (♀: 1 USNM). Puyo 44km s. 21 May 1977 DL & SS Vincent (♂: 5 USNM, ♀: 2 USNM). Puyo 18km n. 1100m 14-8-1982 R. Hensen & A. Aptroot (♂: 1 RNH). **Pichincha:** Tinalandia 800m III-1983 L. Masner & M. Sharkey (♂: 2 PMA). **Zamora:** Río Jumbeo 1-IV-1965 Peña (♂: 5 MCZ, ♀: 2 MCZ). Zamora IV-4-1965 Peña (♂: 1 AEI). Unplaced: Cumbaratza (E) XI-21-1970 Luis E. Peña (♂: 1 AEI). Mera 26-I-1923 F.X. Williams (♂: 1 BISH). **PARAGUAY: Guaira:** w. Villarica, Caballero, I-72 Peña (♂: 1 IIES). Unplaced: Piareta 12-71 Peña (♂: 1 IIES). **PERU: Cuzco:** Agua Calliente 21-28-XII-1983 L. Huggert (♂: 8 PMA, ♀: 1PMA). Machu Picchu 1-XII-1965 H. & M. Townes (♀: 1 AEI). Qunicemil, 750m nr. Marcapata September 1962 Luis Peña (♂: 8 AEI, ♀: 3 AEI). **Huanuco:** Cayumba, 35km s. Tingo Maria 800m 1-XI-1973 J.M. Schunke B.M. 1974-37 (♀: 1 BMNH). Las

Palmas 5km sw. 1000m X-16-1954 E.I. Schlinger & E.S. Ross (♂: 2 CAS). Las Palmas 10mi sw. 1000m IX-26-1954 E.I. Schlinger & E.S. Ross (♀: 4 CAS). Monson Valley, Tingo Maria IX-21-1954 E.I. Schlinger & E.S. Ross (♂: 1 CAS). Monson Valley, Tingo Maria 23-IX-1954 E.I. Schlinger & E.S. Ross (♂: 6 CAS, ♀: 3 CAS). Monson Valley, Tingo Maria X-10-1954 E.I. Schlinger & E.S. Ross (♂: 4 CAS, ♀: 3 CAS). Monson Valley, Tingo Maria X-19-1954 E.I. Schlinger & E.S. Ross (♀: 1 CAS). Monson Valley, Tingo Maria X-21-1954 E.I. Schlinger & E.S. Ross (♂: 1 CAS, ♀: 1 CAS). Monson Valley, Tingo Maria X-26-1954 E.I. Schlinger & E.S. Ross (♀: 1 CAS). Monson Valley, Tingo Maria XI-21-1954 E.I. Schlinger & E.S. Ross (♂: 1 CAS). Monson Valley, Tingo Maria XI-29-1954 E.I. Schlinger & E.S. Ross (♂: 1 CAS, ♀: 1 CAS). Monson Valley, Tingo Maria XII-2-1954 E.I. Schlinger & E.S. Ross (♀: 1 CAS). Tingo Maria 26-29-I-1984 L. Huggert (♂: 14 PMA, ♀: 3 PMA). Tingo Maria 30-I-1984 L. Huggert (♂: 6 PMA, ♀: 1 PMA). Tingo Maria, 1km e. 15-VIII-1971 P.S. & H.L. Broomfield. MT dense woodland B.M. 1971-486 (♀: 1 BMNH). Tingo Maria, 26 mi. e. XII-10-54 1100m E.I. Schlinger & E.S. Ross (♀: 1 CAS). Tingo Maria, 67 mi. e. X-4-54 350m E.I. Schlinger & E.S. Ross (♀: 1 CAS). Tocache 2-II-1984 L. Huggert (♂: 4 PMA, ♀: 1 PMA). **Junin:** Colonia Perene, Río Perene 18 mi ne La Merced I-3-55 E.I. Schlinger & E.S. Ross (♂: 2 CAS, ♀: 1 CAS). Paratuchali 22-I-1984 L. Huggert (♂: 10 PMA, ♀: 4 PMA). Satipo 18-I-1984 L. Huggert (♂: 10 PMA, ♀: 1 PMA). Satipo 19-24-I-1984 L. Huggert (♂: 11 PMA, ♀: 6 PMA). **Lima:** Magdalena [del Mar?] [Lima?] Mar 28-10 CHT Townsend (♀: 1 USNM). **Loreto:** Iquitos, ne. Río Nanay 6-II-1984 L. Huggert (♂: 10 PMA). Iquitos, Gransa UNAP 9-II-1984 L. Huggert (♂: 2 PMA). Iquitos, Quisto Cocha 5-II-1984 L. Huggert (♂: 1 PMA). Iquitos, Barilla 10-II-1984 L. Huggert (♂: 1 PMA). **Madre de Dios:** Laberinto, 70km w. Pto. Maldonado on Río Madre de Dios 1-2-I-

1984 A.T. Finnamore (♀: 1 PMA). Pto. Maldonado 1-11-I-1984 L. Huggert (♂: 50 PMA, ♀: 14 PMA). Tambopata Reserve, 50km s. Pto. Maldonado on Río Tambopata 3-8-I-1984 A.T. Finnamore (♂: 1 PMA, ♀: 1 PMA). **Ucayali:** Tacshitea, 88km n. Pucallpa jct. Río Callaria & Río Ucayali 22-25-I-1984 A.T. Finnamore (♂: 1 PMA). **VENEZUELA:** **Zulia:** El Tucuco, 45km sw. Machiques, 5-6-VI-1976 A.S. Menke & D. Vincent (♀: 1 USNM).

Distribution (Map 18).—Bolivia, Brazil, Ecuador, Paraguay, Peru, Venezuela.

***Incastigmus thoracicus* (Ashmead),
new combination**

Stigmus thoracicus Ashmead 1900:223 ♀. Holotype*: ♀, St. Vincent W.I., H. Smith 238/W. Indies 99-331 (BMNH type Hym 21.885).

Stigmus smithii Ashmead 1900:223 ♀. **New synonymy.** Holotype*: ♂, W. Indies (BMNH type Hym 21.886). 99-331. Ashmead incorrectly sexed the type specimen when he described *smithii* based on a single female. The holotype is a male.

Diagnosis.—The red petiole is sufficient to distinguish this species in lighter colored specimens. Darker (and lighter) specimens are distinguished by the extreme reduction of the median scutal groove, shiny hypoepimeral area, and rounded corners of the transverse pronotal carina.

Description.—Male. Length 3.0-3.8 mm.

Head. Flagellomeres without tyli or specialized setae; basal flagellomere length $2.0 \times$ apical width; penultimate flagellomere length $1.1 \times$ apical width. Head almost uniformly microsculptured; upper frons and vertex with slightly less microsculpture and with sparse obscure punctures. Clypeus obscured by dense appressed setae which extend broadly up inner orbits to height of scape. Micropore field present as discrete patch. Ocelli closer to each other than to eyes. OOD $2.0 \times$ LOD. Gena microsculptured, sparsely punctate, non-carinate, without ventral swelling or tooth. Occipital carina foveolate.

Mesosoma. Pronotum with transverse carina rounded laterally, not toothed or produced; transverse sulcus with evanescent longitudinal carinae; pronotal lobe normal, not toothed; side with several evanescent carinae. Scutum shiny, weakly microsculptured; notaular groove present anteriorly, not elongate; median groove absent, pit evident posteriorly as one of many evanescent fovea in transverse row next to posterior margin; punctures minute, sparse. Scutellum and mesopleuron shiny, without microsculpture; impunctate except sternopleural region with minute sparse punctures; preomalar area with sparse setae; hypersternaulus without foveae; scrobal sulcus and omaulus weakly foveolate. Metapleuron microsculptured on ventral half, otherwise shiny, impunctate. Propodeum shiny, without microsculpture over most of basolateral area and dorsolateral spheres; basolateral area adjacent to metapleuron without sculpture; dorsal enclosure areolae evanescent, areolae small relative to larger evanescent areolae of dorsolateral spheres, the 2 groups of areolae separated by a smooth unsculptured area.

Metasoma. Terga shiny, without microsculpture; punctures sparse, evanescent. Sterna weakly microsculptured, punctures sparse but increasing in density on posterior metasoma.

Color. Light form: ground color black. White: palpi, mandible except apex, spot on pronotal lobe, fore tibia and tarsus, mid tibia and tarsus, hind tibia on basal half or more and tarsus. Yellow-orange: antenna, mesosoma except propodeal dorsum, fore leg basal to tibia, mid leg basal to tibia, hind leg basal to tibia and apex of tibia, petiole except ventral apex, apex of 1 or more sterna. Dark form: ground color black. White: palpi, mandible except apex, spot on pronotal lobe, basal ring of hind tibia. Yellow-brown: antenna, pronotum except dorsally and spot on pronotal lobe, mesopleuron anteriorly, fore leg, mid leg, hind trochanter and tarsus, tegula.

Female. Length 3.9 mm. Similar to male except as follows: basal flagellomere length $3.0 \times$ apical width. Clypeus shiny, with several punctures, setae sparse; clypeal apex with median teeth separated by shallow emargination; median lobe with 2 elongate setae issuing from 2 narrowly separated pits. Inner orbits sparsely setose, not obscuring sculpture. OOD $2.5 \times$ LOD. Color, as above for light form except white on scape and orange on clypeus and propodeal dorsum.

Material Examined (6♂, 5♀).—**DOMINICA:** Pont Casse; Springfield; Springfield Plantation. **GRENADA:** 2500 feet. Balthazar, windward side; Botanical Garden. **ST. VINCENT:** (no other data).

Distribution (Map 19).—Dominica, Grenada, St. Vincent.

LLAQHASTIGMUS Finnamore, new genus (Figs. 36–38)

Derivation of Generic Name.—Llaqha is a Quechua term meaning dark, in reference to the generally black coloration of species in this genus.

Diagnosis.—Females of this genus can be separated from all others in the Stigmina by the enlarged, truncate, apicoventral mandibular tooth. Females in other genera have an acute apicoventral tooth. Males can be separated with a combination of a tridentate mandible and a scutum without a trace of a posteromedian pit or groove. Males in other genera have a bidentate mandible or at least a posteromedian pit on the scutum.

Description.—Head. Labrum bilobed with a small median notch (labrum quadrilobed in 2 species both of which lack a subomaulus). Mandible with apex tridentate; apicoventral tooth in female enlarged, apex truncate; without inner basal tooth. Clypeal apex unmodified in male, without bevelled edge; in female with 4 teeth. Interantennal tubercle absent. Frontal carina absent. Vertex with micropore field between lateral ocellus and com-

pound eye. Inner orbits converging below. Eye not margined by carina. Occipital carina complete, not joining hypostomal carina, simple in female, foveolate in male, otherwise unmodified.

Mesosoma. Scutum without trace of median groove or posteromedian pit; notaular groove normal, not elongate. Acetabular carina intercepting omaulus. Scrobal sulcus often evanescent. Hypoepimeral area without coarse sculpture. Mid basitarsus of male elongate, as long or longer than next 3 tarsomeres combined. Poste-

rior margin of hind tibia with 2 or 3 spines. Fore wing without setae in cellular area. Hind wing media diverging before cu-a; submedian cell of normal size, not reduced.

Metasoma. Petiole carinate. Pygidial plate narrow, absent in male. Digitus elongate.

Type Species.—*Llaqhastigmus jatunkirus* Finnamore, new species.

Distribution (Map 37).—Neotropical, restricted to South America (subtropical highland or montane forest?).

KEY TO SPECIES OF *LLAQHASTIGMUS*

- 1 Male 2
- 1' Female 15
- 2 Gena ventrolaterally and sternopleural region with relatively dense, elongate setae; Peru 13. *shachus* Finnamore, new species
- 2' Gena and sternopleural region sparsely pubescent with short inconspicuous setae 3
- 3 Preomalar area densely setose, obscuring sculpture; mesosoma often extensively red; se. Brazil 8. *mantanti* Finnamore, new species
- 3' Preomalar area sparsely setose; mesosoma black except pronotal lobe which is usually white 4
- 4 Scape, fore femur, and pronotal lobe, black; mesosoma with scrobal sulcus foveolate; clypeus sparsely setose, underlying punctures visible; Ecuador, Colombia 3. *chutiayana* Finnamore, new species
- 4' One or more of scape, fore femur, or pronotal lobe, yellow-brown or white; mesosoma with scrobal sulcus usually smooth, rarely foveolate; clypeus usually obscured by dense appressed setae 5
- 5 Subomaulus absent 6
- 5' Subomaulus present 7
- 6 Petiole with 3 or 4 coarse lateral carinae; Bolivia 2. *australis* Finnamore, new species
- 6' Petiole microcarinate laterally; Ecuador, Colombia 11. *santanderanus* Finnamore, new species
- 7 Scape brown with yellow-brown at base and apex only; flagellum and femora black; propodeum with area adjacent to enclosure finely carinate, lateral spheres without large areolae; transscutellar sulcus with foveae small or absent; scrobal sulcus not foveolate, only slightly impressed; Ecuador 5. *ecuatorialis* Finnamore, new species
- 7' Scape yellow-brown at least ventrally; one or more femora usually yellow to yellow-brown; propodeum with area adjacent to enclosure irregularly sculptured, lateral spheres coarsely areolate; transscutellar sulcus usually with prominent foveae; scrobal sulcus often foveolate 8
- 8 Head and mesosoma coarsely, uniformly microsculptured, dull; microsculpture of frons not distinct from that of vertex; scutum with small evanescent punctures; Peru, Ecuador, Venezuela 9. *muthus* Finnamore, new species
- 8' Vertex, anterior to mid ocellus, more shiny than frons (less microsculpture) and/or mesosoma with mid and lower mesopleuron shiny, without or with little microsculpture; punctuation of scutum distinct or absent 9
- 9 Scutum shiny, without microsculpture on posterior $\frac{2}{3}$; scutellum punctures sparse, min-

- ute, appearing impunctate; scrobal sulcus coarsely foveolate; Ecuador, Colombia, Venezuela 14. *sharkeyi* Finnamore, new species
- 9' Posterior half of scutum microsculptured and/or punctate or scrobal sulcus smooth, without foveae 10
- 10 Pronotal lobe brown to black; posterior half of scutum shiny, punctures sparse; scrobal sulcus only slightly evident, not foveolate; Ecuador, Colombia 10. *nigricollaris* Finnamore, new species
- 10' Pronotal lobe white; posterior half of scutum punctate and/or microsculptured; scrobal sulcus usually foveolate 11
- 11 Transverse sulcus of pronotum without longitudinal carinae, sulcus smooth, usually without sculpture 12
- 11' Transverse sulcus of pronotum with longitudinal carinae 13
- 12 Propodeum with few carinae on lateral sphere, shiny toward metapleuron; petiole (measured dorsally) longer than first tergum; Peru 7. *Ilutanis* Finnamore, new species
- 12' Propodeum with dense irregular carinae on lateral sphere and with microsculpture adjacent to metapleuron; petiole (measured dorsally) shorter than first tergum; Bolivia, Peru 12. *sapanis* Finnamore, new species
- 13 Occipital carina simple, not foveolate or raised ventrally; tarsi white; Ecuador 1. *ambiguus* Finnamore, new species
- 13' Occipital carina at least finely foveolate and usually slightly raised ventrally; tarsi white to yellow brown 14
- 14 Scrobal sulcus coarsely foveolate; scutum coarsely but sparsely punctured in single known specimen; Colombia 4. *colombianus* Finnamore, new species
- 14' Scrobal sulcus finely, if at all, foveolate; scutum finely to coarsely punctured; Venezuela to Bolivia 6. *jatuunkirus* Finnamore, new species
- 15 Gena ventrally and sternopleural region with relatively dense, elongate setae; Peru 13. *shachus* Finnamore, new species
- 15' Gena ventrally and sternopleural region sparsely pubescent with short inconspicuous setae 16
- 16 Fore coxa and usually some of prothorax red; se. Brazil 8. *mantanti* Finnamore, new species
- 16' Prothorax and fore coxa black 17
- 17 Microsculpture of head and scutum uniform throughout; scutum with small obscure punctures; Peru, Ecuador, Venezuela 9. *nuthus* Finnamore, new species
- 17' Microsculpture of vertex not as dense as frons (vertex more shiny); scutum often shiny or with large punctures 18
- 18 Pronotal lobe dark, brown to black 19
- 18' Pronotal lobe white 20
- 19 Scrobal sulcus coarsely foveolate; dorsal mandibular tooth acute; scape black; Ecuador, Colombia 3. *chutiayana* Finnamore, new species
- 19' Scrobal sulcus finely foveolate; dorsal mandibular tooth broad; scape yellow; Ecuador, Colombia 10. *nigricollaris* Finnamore, new species
- 20 Propodeum closely and finely carinate on area adjacent to enclosure; Ecuador 5. *ecuatorialis* Finnamore, new species
- 20' Propodeum coarsely areolate on area adjacent to enclosure 21
- 21 Transverse sulcus of pronotum without longitudinal carinae, smooth, usually without sculpture 22
- 21' Transverse sulcus of pronotum with at least a few longitudinal carinae 23
- 22 Clypeus with elongate specialized setae on apical edge except for narrow median emargination; Peru 7. *Ilutanis* Finnamore, new species
- 22' Clypeus with elongate specialized setae on median and lateral teeth only; Peru, Bolivia 12. *sapanis* Finnamore, new species
- 23 Scutum shiny, without microsculpture on posterior $\frac{2}{3}$; punctures minute, sparse, appear-

- ing impunctate posteriorly; scrobal sulcus foveolate; Ecuador, Venezuela 14. *sharkeyi* Finnamore, new species
- 23' Scutum with microsculpture **and/or** punctures posteriorly; scrobal sulcus foveolate or not 24
- 24 Scrobal sulcus entirely foveolate; clypeal punctures minute, relatively dense and more or less equally distributed on raised area above median teeth; Colombia 4. *colombianus* Finnamore, new species
- 24' Scrobal sulcus usually foveolate anteriorly or not at all, occasionally entirely foveolate; clypeal punctures sparse with relatively large more or less impunctate area above median teeth 25
- 25 Clypeal teeth black; Venezuela to Bolivia 6. *jatunkirus* Finnamore, new species
- 25' Clypeal teeth yellow-brown; Ecuador 1. *ambiguus* Finnamore, new species

1. ***Llaqhastigmus ambiguus*** Finnamore,
new species

Derivation of Name.—The species epithet, *ambiguus*, is from the Latin “ambiguus” meaning of doubtful nature, in reference to the single known locality and lack of material to adequately judge variation.

Diagnosis.—The simple occipital carina that is not raised ventrally or foveolate will distinguish males of this species from all others and females from most other species in the genus. Males of all other species and females of most species have an occipital carina at least slightly raised ventrally bearing at least several foveae. Additionally, female *ambiguus* are without red coloration, have yellow-brown clypeal teeth, normal genal setae, differing microsculpture density between frons and vertex, and scutum with microsculpture and sparse punctures. Females likely to be confused with this species have one or more of the following: clypeal teeth black, mesosoma red in part, setae of lower gena elongate and relatively dense, frons and vertex with uniform microsculpture density, and/or scutum shiny apparently without punctures.

Description.—Male. Length 3.4–4.6 mm.

Head. Sculpture of clypeus obscured by dense appressed setae. Gena ventrally, with sparse straight setae that are subequal to or less than greatest width of fore basitarsus. Microsculpture of frons more dense than that of vertex adjacent to mid

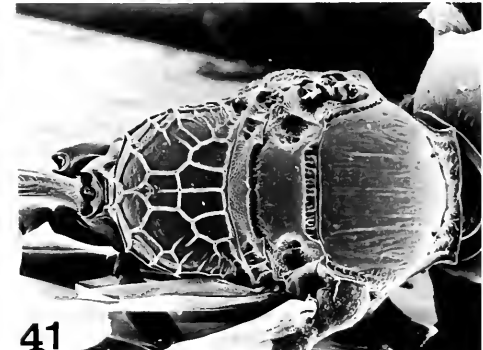
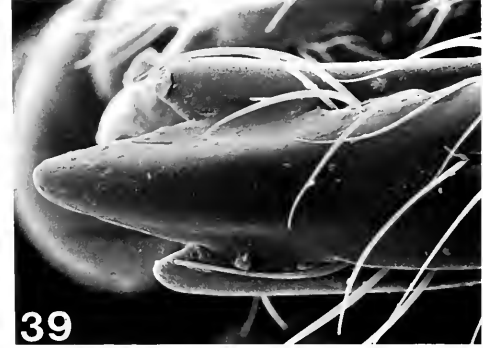
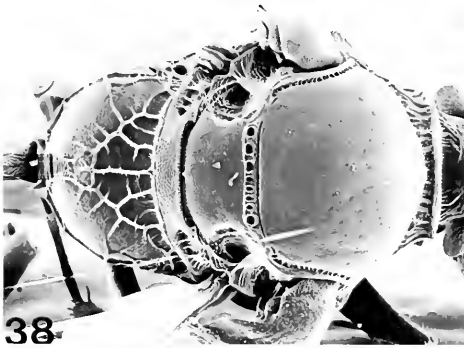
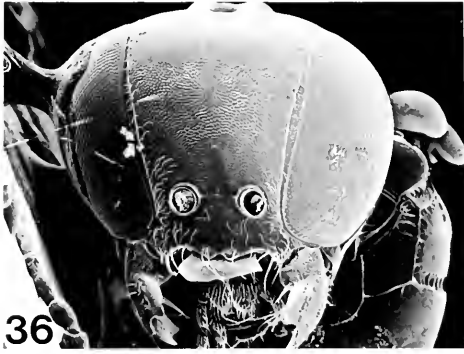
ocellus. Occipital carina simple, not raised ventrally or foveolate.

Mesosoma. Transverse sulcus of pronotum with longitudinal carinae. Scutum microsculptured, with fine sparse punctures more than 5 diameters apart (sometimes interspersed with more coarse, although equally sparse punctures) and concentrated on centre of disc. Transscutellar sulcus foveolate. Preomalar area sparsely setose, setae not obscuring underlying sculpture. Subomalar present. Scrobal sulcus usually with irregular foveae on at least anterior third; foveae variable from almost absent to present on entire scrobal sulcus. Sternopleural region microsculptured with sparse (apparently absent) setae. Propodeum shiny, area adjacent to enclosure and lateral sphere with several large areolae composed of relatively low carinae.

Metasoma. Petiole with 3 or 4 coarse carinae laterally.

Color. Ground color black. White: mandible except apically, palpi, pronotal lobe, tarsi. Yellow to yellow-brown: antenna (generally yellow ventrally to brown dorsally on apical flagellomeres), tegula, fore and mid legs except tarsi, wing veins, apical metasomal sterna. Brown: mandibular apex, stigma of fore wing, hind leg except tarsus.

Female. Length 3.9 mm. Similar to male except as follows: apicoventral mandibular tooth enlarged, truncate, much larger



Figs. 36–41. *Llaqhastignus* and *Stignus*. 36, *Llaqhastignus jatunkirus* ♀, head, frontal view. 37, *L. jatunkirus* ♀, mandible, outer view. 38, *L. jatunkirus* ♀, mesosoma, dorsal view. 39, *Stignus* sp. ♀, mandible, outer view. 40, *Stignus* sp. ♀, head, frontal view. 41, *Stignus* sp. ♀, mesosoma, dorsal view.

than other teeth. Clypeal apex quadridentate as follows: a lateral lobe flanking lateral edge of labrum, a pair of smaller median teeth separated from lateral lobes by broad emarginations and separated from each other by a narrow U-shaped emargination. Clypeal apex with specialized flattened, elongate, setae on teeth but absent from emarginate interspaces; 2 setae

per median tooth and 6–7 on lateral lobe. Clypeus shiny, microsculpture absent, punctures 3–4 diameters apart on disc. Apical margin of clypeus yellow-brown.

Material Examined (27♂, 1♀).—Holotype: ♀, ECUADOR: Pich. Prov. Guayllabamba, 10km n. on Río Pisque, 2500m II-1983. M. Sharkey, L. Masner (BRD). Paratypes: ECUADOR: Pichincha: Guay-

llabamba, 10km n. on Río Pisque, 2500m II-1983. L. Masner, M. Sharkey (δ : 2 BRD, 2 PMA). 10km n. Guayllabamba 26-II-1983. Masner & Sharkey (δ : 4 BRD, 19 PMA).

Distribution.—(Map 20). Ecuador.

2. *Llaqhastigmus australis* Finnamore, new species

Derivation of Name.—The species epithet is derived from the Latin "austral" meaning southern in reference to the southern locality of the only known specimen.

Diagnosis.—Female unknown. Male: labrum quadrilobed with a deep median notch; subomaulus absent, petiole coarsely carinate (carinae normal) laterally. *L. australis* and *santanderanus* are the only species in the genus lacking a subomaulus and having a quadrilobed labrum (at least in males, females for both species are unknown). In all other species in the genus the subomaulus is present and the labrum is bilobed with a slight median emargination.

Description.—Male. Length 5.0 mm.

Head. Sculpture of clypeus obscured by dense appressed setae. Labrum quadrilobed with a deep median emargination. Gena ventrally, with sparse straight setae that are subequal to or less than greatest width of fore basitarsus. Microsculpture of frons more dense than that of vertex. Occipital carina raised ventrally and finely foveolate at least ventrally.

Mesosoma. Transverse sulcus of pronotum with longitudinal carinae. Scutum microsculptured, punctures sparse more or less evenly distributed and separated by 5–10 puncture diameters. Transscutellar sulcus not foveolate. Preomalar area sparsely setose, setae not obscuring underlying sculpture. Subomaulus absent, represented as an evanescent ridge near posteroventral apex of pronotum, not carinate or intersecting omaulus. Scrobal sulcus weakly impressed anteriorly, attenuated posteriorly, not foveolate. Sternopleural region shiny without microsculp-

ture, sparsely punctate, sparsely setose. Propodeum shiny, area adjacent to enclosure without microsculpture, with several large areolae composed of low carinae; lateral sphere shiny, with evanescent microsculpture, areolae smaller.

Metasoma. Petiole with 3 coarse lateral carinae.

Color. Ground color black. White: mandible except apically, palpi, pronotal lobe. Yellow-brown: scape, pedicel, fore and mid legs except coxae, hind tibia and tarsus, tegula, apical metasomal sterna.

Female. Unknown.

Material Examined (1 δ).—Holotype: δ , BOLIVIA: Cochabamba, Prov. Carrasco, Empalme 3000m II-1971. Fritz y Martinez (IIES).

Distribution (Map 21).—Bolivia.

3. *Llaqhastigmus chutiyana* Finnamore, new species

Derivation of Name.—The species epithet is derived from the Quechua terms "ch'uti", meaning naked and "yana", meaning black, in reference to the relatively hairless condition of this black species.

Diagnosis.—The combination of the black scape and pronotal lobe, scrobal sulcus foveolate, and the apicodorsal mandibular tooth of female acute (normal) will separate this species from all others in the genus. All other species except *nigricollaris* have a white pronotal lobe. *L. chutiyana* is distinguished from *nigricollaris* by the black scape, foveolate scrobal sulcus and acute apicodorsal mandibular tooth in the female; *nigricollaris* has a yellow-brown scape, partially foveolate scrobal sulcus and enlarged apicodorsal mandibular tooth in the female.

Description.—Male. Length 3.9–5.0 mm.

Head. Sculpture of clypeus not obscured by setae. Clypeus shiny without microsculpture, setae and punctures sparse and at least 1 diameter apart on disc. Gena ventrally with evanescent microsculpture, punctures and setae sparse,

setae less than greatest width of fore basitarsus. Microsculpture of frons more dense than that of vertex. Occipital carina raised ventrally and foveolate on at least that area.

Mesosoma. Transverse sulcus of pronotum with longitudinal carinae. Scutum microsculptured, punctures small and sparse, punctures more or less evenly distributed although somewhat less dense on posterior disc. Transscutellar sulcus foveolate. Preomalar area asetose. Subomalar present. Scrobal sulcus coarsely foveolate. Sternopleural region shiny often with evanescent microsculpture, punctures sparse and minute. Propodeum shiny without microsculpture, area adjacent to enclosure and lateral sphere with large areolae composed of relatively high carinae.

Metasoma. Petiole with 2 or 3 lateral carinae.

Color. Ground color black. Yellow-brown to brown: mandibles except apically, palpi, fore and mid tibiae and tarsi, hind tibia on inner side and tarsus, tegula, apical metasomal sterna.

Female. Length 4.1–4.4 mm. Similar to male except as follows: apicoventral mandibular tooth enlarged, truncate and much larger than other teeth. Clypeal apex quadridentate as follows: lateral lobe flanking edge of labrum, pair of smaller median teeth separated from lateral lobe by deep emargination and from each other by U-shaped notch. Clypeal apex with 4 specialized, flattened, elongate setae on lateral lobe and 2 per median tooth, setae absent from emarginate interspaces. Clypeus shiny, microsculpture absent; punctures sparse, 3 or more diameters apart. Apical margin of clypeus black.

Material Examined (8♂, 3♀).—Holotype: ♂, ECUADOR: Tungurahua, Banos 2,000m. 21-X-1974. M. Cooper B.M.1975–33 (BMNH). Paratypes: **COLOMBIA: Valle:** Penas Blancas 22-Xi-1974–1. R. Wilkerson. Malaise Trap (♀: 1 FSCA). **ECUADOR: Tungurahua:** Banos 2,000m. 17-X-

1974. M. Cooper B.M.1975–33 (♂: 1 BMNH). Banos 2,000m. 21-X-1974. M. Cooper B.M.1975–33 (♂: 2 BMNH, 1 PMA). Banos. c.2,000m. 7-X-1978. M. Cooper B.M. 1979–20 (♀: 2 BMNH). Banos. c.2000m 19-XI-1978 M. Cooper B.M. 1979–20 (♂: 2 BMNH). Banos;—Tungurahua Norths.:2300m; Leg. R. Hensen et A. Ap- troot; 11–8–1982 (♂: 1 RNH).

Distribution.—(Map 22). Colombia, Ecuador.

4. *Llaqhastigmus colombianus*

Finnamore, new species

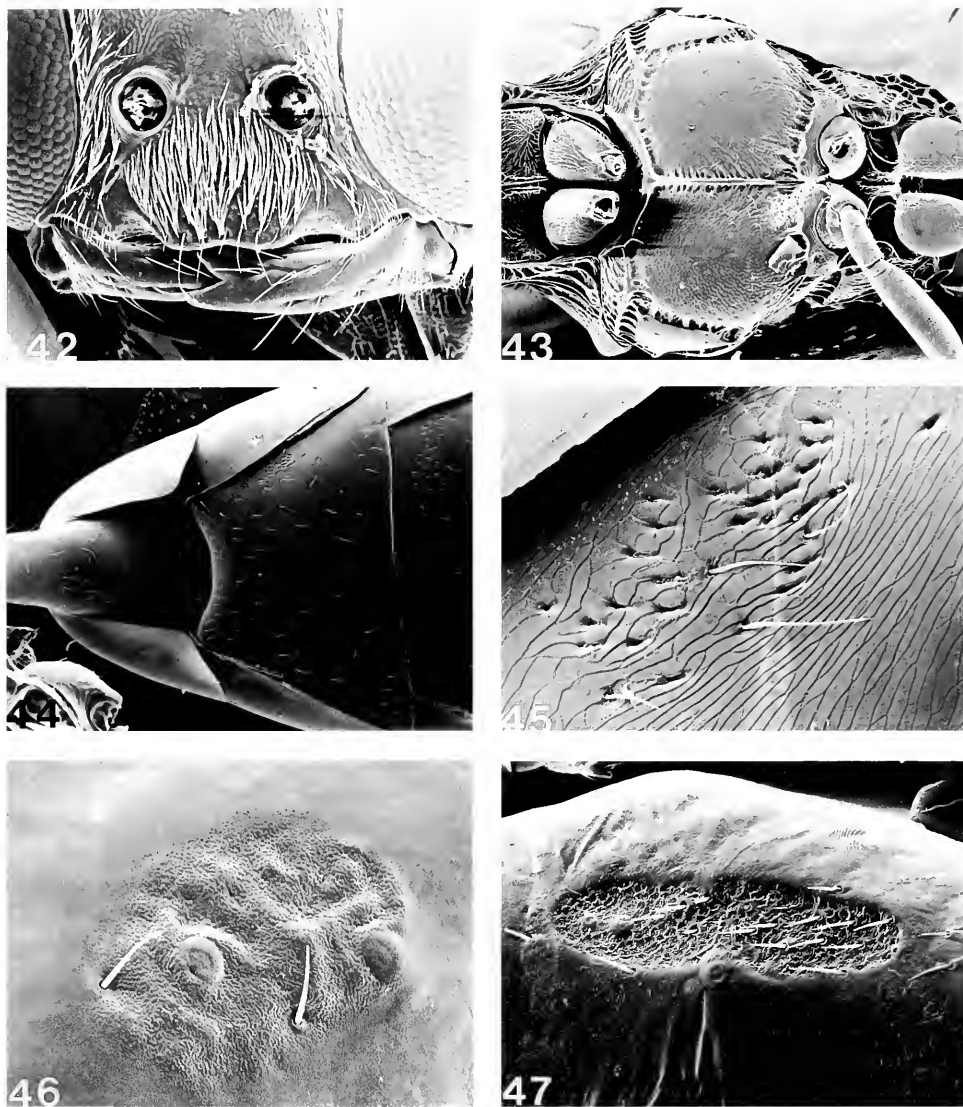
Derivation of Name.—The species epithet, *colombianus*, is derived from the country Colombia, where all specimens of this species have been collected.

Diagnosis.—The following combination will separate this species from others in the genus. Occipital carina foveolate ventrally, pronotum black except white pronotal lobe, coarsely foveolate scrobal sulcus usually with 3 or 4 large foveae and sulcus usually diminishing in width posteriorly, and female clypeus with fine punctures about 2 diameters apart and equally distributed on median third. This species is similar to *jatunkirus* and *sharkeyi* from which it differs with the coarsely foveolate scrobal sulcus and in the female with the homogeneously punctate median clypeal region.

Description.—Male. Length 3.9 mm.

Head. Sculpture of clypeus obscured by dense appressed setae. Gena ventrally with sparse straight setae that are subequal to or less than greatest width of fore basitarsus. Microsculpture of frons more dense than that of vertex. Occipital carina raised ventrally and foveolate.

Mesosoma. Transverse sulcus of pronotum with longitudinal carinae. Scutum microsculptured, punctures sparse and relatively coarse. Transscutellar sulcus foveolate. Preomalar area sparsely setose, setae not obscuring underlying sculpture. Subomalar present. Scrobal sulcus with 3 or 4 coarse foveae, sulcus



Figs. 42–47. *Stigmus*, *Tzustigmus* and *Incastigmus* 42, *Stigmus* sp. ♂, clypeus, showing lateral bevels. 43, *Stigmus* sp. ♂, mesosoma, ventral view. 44, *Tzustigmus syam* ♀, metasomal sternum 2. 45, *T. syam* ♀, micropore field on metasomal sternum 2. 46, *Incastigmus inti* ♂, micropore field on fore wing stigma. 47, *T. syam* ♀, micropore field on fore wing stigma.

entirely foveolate, somewhat narrower posteriorly. Sternopleural region weakly microsculptured, punctures and setae sparse almost absent from lower area. Propodeum shiny, area adjacent to enclosure and lateral sphere with several large areolae composed of relatively low carinae.

Metasoma. Petiole with several carinae laterally.

Color. Ground color black. White: pronotal lobe. Yellow-brown: palpi, mandible except apically, antenna, tegula, stigma, fore and mid legs except coxae, hind tarsus, apical metasomal tergum. Brown: hind leg except tarsus.

Female. Length 3.8–4.7 mm. Similar to male except as follows: apicoventral mandibular tooth enlarged, truncate, much

larger than other teeth. Clypeal apex quadridentate as follows: lateral lobe flanking lateral edge of labrum, pair of smaller median teeth separated from lateral lobes by broad emarginations and separated from each other by broad U-shaped notch. Clypeal apex with specialized flattened, elongate, setae on teeth and most of emarginate interspaces; with 2 setae per median tooth, 3 per lobe and 3 on lateral emarginations. Clypeus shiny, without microsculpture, punctures sparse laterally but raised median area evenly and finely punctate with punctures up to 3 diameters apart, no part of median raised area without punctures. Apical clypeal margin black. Scutum sometimes without microsculpture on disc. Antenna and legs more brown than male.

Material Examined (1♂, 8♀).—Holotype ♀, COLOMBIA: Dept. Valle, Penas Blancas 1750m 10km w. Cali, very wet premontane forest, R.C. Wilkerson 29-I-1975 Malaise Trap (FSCA). Paratypes: **COLOMBIA: Antioquia:** Antioquia 1800m 13–22-IV-1973 (♀: 1 PMA). **Caqueta:** Florencia 480m 31-X-5-XI-1971 M. Cooper B.M. 1972–275 (♀: 1 BMNH). **Valle:** Pance 19-XI-1974–1 R. Wilkerson Malaise Trap (♀: 1 FSCA). Pance CVC (1700m) 15km w. Cali, very wet premontane forest, R.C. Wilkerson 23-XII 1974 (♂: 1 FSCA, ♀: 3 FSCA). Pance CVC (1700m) 15km w. Cali, very wet premontane forest, R.C. Wilkerson 28-X-1974 Malaise Trap (♀: 1 FSCA). Penas Blancas 21-XI-1974–3 R. Wilkerson Malaise Trap (♀: 1 FSCA).

Distribution (Map 23).—Colombia.

5. *Llaqhastigmus ecuatorialis*

Finnamore, new species

Derivation of Name.—The species epithet is derived from a combination of the country of origin of the specimens, Ecuador, and the English word equator in reference to the distribution of the species.

Diagnosis.—The combination of a brown scape that is yellow-brown at base and apex, and a scrobal sulcus that is absent

or weakly impressed and without foveae will separate this species from all others in the genus. All other species, except *chutiyana* and *santanderanus* have the scape yellow ventrally and often a foveolate scrobal sulcus. *Llaqhastigmus chutiyana* has a black pronotal lobe while *santanderanus* lacks a subomaulus; *ecuatorialis* has a white pronotal lobe and a subomaulus is present. This species also has finely carinate sculpture on the propodeum adjacent to enclosure further distinguishing it from other species.

Description.—Male. Length 3.9–4.3 mm.

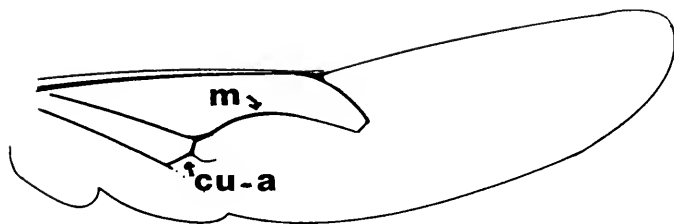
Head. Clypeal sculpture obscured by dense appressed setae. Gena ventrally, with sparse straight setae that are subequal to or less than greatest width of fore basitarsus. Microsculpture of frons more dense than that of vertex. Vertex microsculpture in some specimens is unusually dense but never as dense as that of frons. Occipital carina ventrally raised and foveolate.

Mesosoma. Transverse sulcus of pronotum with longitudinal carinae. Scutum microsculptured, with sparse scattered punctures. Transscutellar sulcus finely foveolate or foveae absent. Preomalar area sparsely setose, setae not obscuring underlying sculpture. Subomaulus present. Omaulus present but in one specimen attenuated ventrally and not reaching acetabular carina. Scrobal sulcus evanescent, slightly impressed, not foveolate. Hypopimeral area microsculptured. Sternopleural region shiny without microsculpture, punctures and setae sparse. Propodeum with microsculpture especially outside enclosure, area adjacent to enclosure and propodeal side with fine irregular carinae which meet dorsolaterally to form small irregular areolae composed of low carinae.

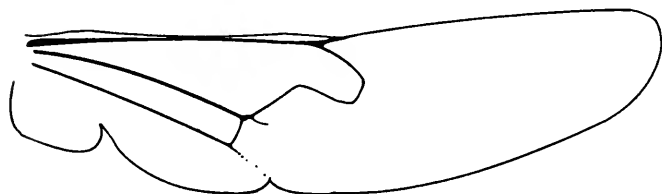
Metasoma. Petiole with 3 or 4 carinae laterally.

Color. Ground color black. White: mandible basally, pronotal lobe. Yellow to yellow-brown: palpi, scape on basal and api-

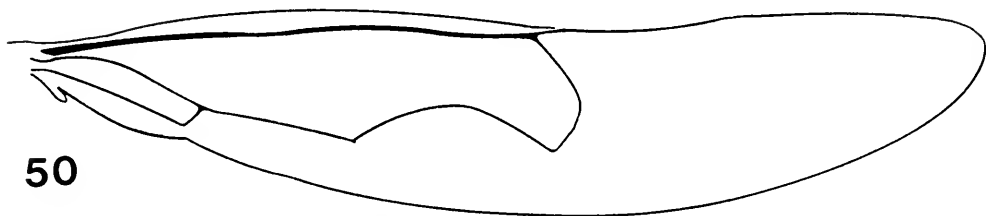
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Figs. 48–50. Stigmina, hind wing. 48, *Llaqhastigmus*. 49, *Tzustigmus*. 50, *Carinostigmus*.

cal ring, sometimes pedicel, tegula, legs except coxae and femora. Brown: scape except basal and apical ring, femora.

Female. Length 4.5 mm. Similar to male except as follows: apicoventral mandibular tooth enlarged, much larger than other teeth. Clypeal apex quadridentate as follows: acutely triangular lateral tooth flanking lateral edge of labrum and surpassing median teeth; pair of smaller median teeth separated from lateral teeth by broad U-shaped emarginations and separated from each other by narrow U-shaped notch. Clypeal apex with specialized, flattened, elongate setae present on teeth but absent from most of emarginate interspace with the exception of single seta on emargination near lateral tooth. Clypeus shiny, with evanescent microsculpture on upper median area only,

punctures sparse and present only on median area. Lateral clypeal tooth red at apex. Both known females have omaulus which is attenuated ventrally and widely separated from acetabular carina. This character is variable in the male (omaulus usually intersecting acetabular carina) and may also be so in the female.

Material Examined (11♂, 2♀).—Holotype: ♂, ECUADOR: Los Duendes, S. Bolivar 10-VI-1965 Peña (MCZ). Paratypes: **ECUADOR: Imbabura:** Otavalo; -Quichinche-2700m Leg. R. Hensen et A. Aptroot 8–7–1982 (♂: 1 RNH). S. Otavalo 3300m I-8–9–1971 Luis E. Peña (♀: AEI). **Pichincha:** San Rafael ca. Quito 2500m 21–29-VI-1975 Col. C. Porter (♀: 1 LILLO). **S. Bolivar:** same data as holotype (♂: 6 MCZ, 1 PMA). **Tungurahua:** Banos, Tungurahua Norths. 2300m Leg. R. Hensen et A. Ap-

troot 11–8–1982 (♂: 1 RNH). Río Chota VI-10–1965 1800m Luis Peña. (♂: 1 AEI).

Distribution (Map 24).—Ecuador.

6. **Llaqhastigmus jatunkirus** Finnamore, new species

Derivation of Name.—The species epithet is derived from two Quechua words; “jatun” meaning large and “kiru” meaning tooth, referring to the enlarged apicoventral mandibular tooth in the female of this species.

Diagnosis.—The following combination of characters will separate this species from all others in the genus. Scape yellow-brown, vertex microsculpture of less density than that of frons, lower gena without modified setae, occipital carina raised ventrally and foveolate, transverse pronotal sulcus longitudinally carinate, pronotal lobe white, scutum microsculptured, submaulus present, preomalar area sparsely setose, scrobal sulcus impressed and finely if at all foveolate, and propodeum areolate on dorsolateral area outside enclosure. Females in addition to the foregoing, have the median clypeal area mostly impunctate apically and punctate basally.

Description.—Male. Length 3.7–5.0 mm.

Head. Sculpture of clypeus obscured by dense appressed setae. Gena ventrally, with sparse straight setae that are subequal to or less than greatest width of fore basitarsus. Microsculpture of frons more dense than that of vertex adjacent to mid ocellus. Occipital carina ventrally raised and foveolate.

Mesosoma. Transverse pronotal sulcus with longitudinal carinae. Scutum microsculptured, punctures sparse with density and size variable. Transscutellar sulcus foveolate. Preomalar area sparsely setose, setae not obscuring underlying sculpture. Submaulus present. Scrobal sulcus impressed with foveae variable from complete to absent, usually anterior half of sulcus weakly foveolate but rarely entirely foveolate or rarely without fove-

ae. Sternopleural region shiny, with at most evanescent microsculpture, punctures small and sparse, setae sparse. Propodeum shiny, area adjacent to enclosure and lateral sphere with several large, somewhat irregular areolae composed of low lying carinae; side without sculpture adjacent to enclosure.

Metasoma. Petiole with 3 or 4 coarse lateral carinae.

Color. Ground color black. White: palpi, pronotal lobe. Yellow-white: tarsi. Yellow to yellow-brown: mandible basally, scape and pedicel usually entirely but at least ventrally, basal flagellomeres ventrally, fore and mid legs except coxae and tarsi, sometimes hind tibia, tegula, tergum VI on apical half or more and VII, sternum VI and VII. Brown: usually hind leg except tarsi and occasionally tibia.

Female. Length 3.8–5.1 mm. Similar to male except as follows: apicoventral mandibular tooth enlarged, truncate, much larger than other teeth. Clypeal apex quadridentate as follows: lateral lobe flanking edge of labrum, pair of median teeth separated from lateral lobe by broad emargination and separated from each other by U-shaped notch. Clypeal apex with specialized, flattened, elongate setae distributed on teeth and often in emarginate interspaces. Clypeus shiny, microsculpture absent, both lateral and median areas sparsely punctate and impunctate apicomediaally. Clypeal teeth black.

Material Examined (38♂ 63♀).—Holotype: ♀, VENEZUELA: Merida: Merida, Sta. Rosa 2000m 15-V-15-VI-1981 A. Briceño & F. Suarez (BRD). Paratypes: **BO-LIVIA: La Paz:** Chulumani 1,700m. 25-III-1979 M. Cooper B.M. 1979–216 (♀: 2 BMNH). Chulumani 1,700m. 30-III-1979 M. Cooper B.M. 1979–216 (♂: 1 BMNH, ♀: 1 BMNH). Chulumani 1,700m. 2-IV-1979 M. Cooper B.M. 1979–216 (♀: 1 BMNH, 1 NMW). **COLOMBIA: Cauca:** Popayan, 1,800m. 10-X-1974 M. Cooper B.M. 1975–33 (♂: 2 BMNH, ♀: 1 BMNH). **Santander del Norte:** Prima 1,700m 29-V-1965 J. & B.

Bechyne (♀: 1 UCV). **Valle Prov.:** summit w. of Cali 6-II-1977 2000m M. Breed, C.D. Michener (♀: 1 SEM). **ECUADOR: Loja:** Loja III-23-26-1965 Luis Peña (♂: 1 AEI). **Pastaza:** 22km sw. Puyo 900m 14-16-VII-1976 S. & J. Peck, forest (♀: 2 BRD). Río Jumbeo (Zamora) 1-IV-1965 Peña (♂: 1 MCZ). **PERU: Cuzco:** Agua Calliente 21-28-XII-1983 L. Huggert (♀: 3 PMA). Machu Picchu 1900m. IX-4/19-1964 C.C. Porter (♀: 3 MCZ). Machu Picchu XI-29-1965 H. & M. Townes (♂: 1 AEI, ♀: 2 AEI). Machu Picchu XII-1-1965 H. & M. Townes (♂: 4 AEI, ♀: 4 AEI). Machu Picchu II-24-27-1968 A. Garcia & C. Porter (♀: 1 MCZ). Machu Picchu (ruins) 2400m 20-IV-1983 C. & M. Vardy B.M. 1983-217 (♀: 1 BMNH). **Huanuco:** Tingo Maria, 26 mi. e. XII-10-1954 1100m E.I. Schlinger & E.S. Ross (♀: 1 CAS). Tingo Maria, 40 mi. s. Carpath Mts. XII-28-1954 E.I. Schlinger & E.S. Ross (♀: 1 CAS). **Pasco:** Oxapampa 2,200m 6-III-1979 M. Cooper B.M. 1979-216 (♀: 1 BMNH). Oxapampa 2,200m 8-III-1979 M. Cooper B.M. 1979-216 (♂: 1 BMNH). **VENEZUELA: Lara:** Yacambu 1200m V-3-1981 H.K. Townes (♂: 3 AEI). Yacambu 1200m V-7-1981 H.K. Townes (♂: 6 AEI, ♀: 11 AEI). Yacambu 1200m V-10-1981 H.K. Townes (♀: 3 AEI). Yacambu 1200m V-13-1981 H.K. Townes (♀: 5 AEI). Yacambu N.P. 1200m cloud forest 7-V-1981 H. Townes (♂: 4 PMA, ♀: 2 PMA). Yacambu N.P. 1200m cloud forest 10-V-1981 H. Townes (♂: 2 PMA, ♀: 1 PMA, 1 BRD). Yacambu 1200m cloud forest 13-V-1981 H. Townes (♂: 3 PMA). **Merida:** Merida 1800m 11-V-1981 L. Masner 1984.149 (♂: 2 PMA, ♀: 7 PMA). Merida, small valley across R. Chama 6-V-1981 L. Masner 1984.157 (♀: 1 PMA). Merida, Sta. Rosa 2000m 3-13-V-1981 L. Masner pan t (♂: 1 PMA). Merida, Sta. Rosa 2000m 15-V-15-VI-1981 A. Briceno & F. Suarez (♂: 1 PMA). Merida, Sta. Rosa 2000m 15-VI-15-VII-1981 A. Briceno & F. Suarez (♂: 2 PMA). Merida, Sta. Rosa 2000m 15-VII-15-VIII-1981 A. Briceno & F. Suarez (♂: 2 PMA). Mucuy nr. Tobay 2200m cloud for-

est 5-V-1981 L. Masner (♂: 1 PMA). Tobay 2,200m IV-30-1981 H.K. Townes (♂: 2 AEI). Tobay 2,200m V-1-1981 H.K. Townes (♀: 1 AEI). Valle de Culata Ruta 7, 18-VII-1988 C. Porter & L. Stange (♂: 1 FSCA).

Distribution (Map 25).—Venezuela to Bolivia.

7. *Llaqhastigmus llutanis* Finnamore, new species

Derivation of Name.—The species epithet is derived from the Quechua "llutan" meaning strange, in reference to the unusual unsculptured transverse pronotal sulcus.

Diagnosis.—This species can be distinguished by the combination of the transverse sulcus of pronotum without carinae, propodeum with lateral sphere mostly unsculptured and crossed by only 1 or 2 low carinae, and female clypeal edge with elongate specialized setae along most of margin. This species is most similar to *sapanis* both of which differ from all others in the genus by their smooth unsculptured transverse pronotal sulcus. The other diagnostic characters will separate these 2 closely related species.

Description.—Male. Length 4.4–4.5 mm.

Head. Sculpture of clypeus obscured by dense appressed setae. Gena ventrally, with sparse straight setae subequal to or less than greatest width of fore basitarsus. Microsculpture of frons more dense than that of vertex adjacent to mid ocellus. Occipital carina ventrally, raised and foveolate.

Mesosoma. Transverse pronotal sulcus smooth, without sculpture. Scutum microsculptured, punctures sparse but occasionally relatively coarse. Transscutellar sulcus foveolate. Preomalar area sparsely setose, setae not obscuring underlying sculpture. Subomalar present. Scrobal sulcus weakly impressed, smooth, not foveolate. Sternopleural region shiny to weakly microsculptured, punctures sparse. Propodeum shiny, area adjacent to

enclosure mostly unsculptured, lateral sphere crossed by at most a few low carinae forming large areolae.

Metasoma. Petiole with 2 fine carinae defining lateral region.

Color. Ground color black. White: palpi, pronotal lobe. Yellow to yellow-brown: mandibles except apically, scape, pedicel, at least ventrally on basal flagellomeres but sometimes entire undersides, fore and mid legs except coxae and femora, hind trochanter and tarsus. Brown: femora, hind tibia.

Female. Length 5.0 mm. Similar to male, except as follows: apicoventral mandibular tooth enlarged, truncate, much larger than other teeth. Clypeal apex quadridentate as follows: lateral lobe flanking lateral edge of labrum, pair of smaller median teeth separated from lateral lobe by broad emargination and separated from each other by narrow U-shaped notch. Clypeal apex with specialized, elongate, flattened setae distributed over all but median notch. Clypeus shiny, microsculpture absent, punctures dense laterally and sparse medially with impunctate area above median teeth. Apical clypeal margin red.

Material Examined (3♂, 1♀).—Holotype: ♀, PERU: Machu Picchu XI-30-1965 H. & M. Townes (AEI). Paratypes: **PERU: Cuzco:** Machu Picchu XI-29-1965 H. & M. Townes (♂: 1 AEI). Machu Picchu XI-30-1965 H. & M. Townes (♂: 1 AEI, 1 PMA).

Distribution (Map 26).—Peru.

8. *Llaqhastigmus mantanti* Finnamore, new species

Derivation of Name.—The species epithet *mantanti* is derived from two Quechua words, "manta" a preposition meaning "from" and "anti" meaning "east". The name refers to the distribution of this species in eastern Brazil.

Diagnosis.—The preomalar area sculpture that is obscured by setae in male and partially obscured by setae in female will separate this species from all others in the genus. Although females of this species

have the sculpture of the preomalar area only partially obscured by setae, they still have greater density of setae on the preomalar area than other species except for *shachus* which has elongate setae. Additionally almost all specimens of this species have some red coloration on the mesosoma. The red coloration is variable, rarely absent but almost always present on fore coxa and lateral pronotum and can extend over most of mesosoma except the propodeum. It is the only species in the genus with red on the mesosoma. Finally the female has an apicoventral mandibular tooth only slightly enlarged in comparison with the median and dorsal teeth. Females of all other species in the genus have a greatly enlarged apicoventral mandibular tooth. As a consequence of the small apicoventral mandibular tooth, females of this species can be confused with those of *Incastigmus*. The bilobed labrum with a small median notch indicate this species is a *Llaqhastigmus* rather than *Incastigmus* which has a quadrilobed labrum.

Description.—Male. Length 4.6–4.9 mm.

Head. Sculpture of clypeus obscured by dense appressed setae. Gena ventrally, with sparse straight setae that are subequal to or less than greatest width of fore basitarsus. Microsculpture of frons more dense than that of vertex adjacent to midocellus. Occipital carina ventrally, raised and foveolate.

Mesosoma. Transverse sulcus of pronotum carinate. Scutum microsculptured, sometimes shiny medially, punctures sparse, posterior margin with transverse row of short carinae. Transscutellar sulcus foveolate. Sculpture of preomalar area obscured by dense appressed setae that are usually continued along midventral line to mid coxae. Subomalarus present. Scrobal sulcus impressed, foveolate. Sternopleural region shiny, weakly microsculptured, sparsely punctate, with increasing setal density ventrally. Propodeum usually microsculptured and usu-

ally with relatively small areoleae adjacent to enclosure that are composed of relatively coarse carinae. Some specimens have larger more typical areolae adjacent to enclosure.

Metasoma. Petiole, laterally smooth or with several fine carinae.

Color. Ground color black. White: palpi, base of mandible, pronotal lobe, at least fore tarsus, sometimes all tarsi. Yellow to yellow-brown: antenna, mandible medially, tegula, legs except at least fore tarsus and sometimes hind femur and tibia. Red: at least pronotal side to entire mesosoma except legs, pronotal lobe, tegula and propodeum; all males have some mesosomal red coloration. Brown: occasionally hind femur and tibia.

Female. Length 4.8–5.0 mm. Similar to male except as follows: apicoventral mandibular tooth enlarged, but only slightly larger than other teeth. Clypeal apex quadridentate with lateral lobe flanking lateral edge of labrum, pair of small median teeth separated from lateral lobe by broad emargination and separated from each other by U-shaped notch. Apical clypeal edge with specialized, elongate, flattened setae on teeth but not on emarginate interspaces (2 setae per median tooth and 4 per lateral lobe). Clypeus shiny, microsculpture absent, punctures variable from almost absent to sparsely distributed over entire surface.

Material Examined (6♂, 19♀).—Holotype: ♀, BRAZIL: Caruaru, Pernambuco 900m IV-1972 M. Alvarenga (BRD). Paratypes: **BRAZIL: Bahia:** 7-VIII-1983 Cepec Itabuna F.P. Benton (♀: 1 BMNH). **Guanabara:** Floresta da Tijuca IV-1966 Alvarenga & Seabra (♀: 1 AEI). Represa Río Grande, Guanabara XII-1967 F.H. Oliveira (♀: 1 BRD). Represa Río Grande I-1968 M. Alvarenga (♀: 2 PMA). Represa Río Grande II-1972 F.M. Oliveira (♀: 2 PMA). Represa Río Grande VII-1972 M. Alvarenga (♀: 2 BRD). **Minas Gerais:** Serra do Caraca, Sta. Barbara I-1970 (♀: 1 PMA). Serra do Caraca, S. Barbara III-1971 F.M. Oliv-

eira (♀: 1 PMA). **Parana:** Campina Grande nr. Curitiba II-23-1966 H. & M. Townes (♂: 1 AEI). **Pernambuco:** Caruaru IV-1972 M. Alvarenga (♀: 2 PMA). Caruaru V-1972. J. Lima (♀: 1 PMA). Curuaru [sic] 900m IV-1972 (♀: 1 BRD). **Río de Janeiro:** III-5-1966 H. & M. Townes (♀: 1 AEI). Guanabara II-1972. M. Alvarenga (♀: 1 PMA). Mangaratiba, Muriqui VII-1969 M. Alvarenga (♀: 1 AEI). Teresopolis III-12-1966 H. & M. Townes (♂: 1 AEI). **Santa Catarina:** Nova Teutonia 27°11'B.52°23'L. 8-X-1937 Plaumann. B.M.1938-312 (♂: 1 BMNH). **Sao Paulo:** Sao Paulo XII-31-1968 V.N. Alin (♂: 1 USNM). San Paulo 20-I-1978 [label in Russian] (♂: 2 ZMMU).

Distribution (Map 27).—Southeastern Brazil.

9. *Llaqhastigmus muthus* Finnamore, new species

Derivation of Name.—The species epithet is derived from the Quechua "muthu" which means dull, in reference to the degree of microsculpture found on members of this species.

Diagnosis.—The dense uniform microsculpture on the head (except clypeus) and mesosoma (except sometimes sternopleural region and propodeum) will separate this species from all others in the genus. In all other species the microsculpture of the frons is of greater density than that of the vertex.

Description.—Male. Length 3.5–4.0 mm.

Head. Sculpture of clypeus obscured by dense appressed setae. Gena ventrally, with sparse straight setae that are subequal to or less than greatest width of fore basitarsus. Microsculpture of frons and vertex of uniform (subequal) density. Occipital carina ventrally, slightly raised and finely foveolate.

Mesosoma. Transverse sulcus of pronotum with longitudinal carinae. Scutum densely microsculptured, impunctate. Transscutellar sulcus foveolate. Preomallear area sparsely setose, setae not obscuring underlying sculpture. Subomaulus

present. Scrobal sulcus weakly impressed with evanescent usually irregular foveae best developed anteriorly. Sternopleural region densely microsculptured, impunctate. Propodeum weakly microsculptured to shiny; area adjacent to enclosure and lateral area carinate; carinae converging dorsolaterally to form small irregular areolae.

Metasoma. Petiole with several coarse carinae laterally.

Color. Ground color black. White: palpi, mandible except apically, pronotal lobe. Yellow to yellow-brown: scape, pedicel and basal flagellomeres ventrally, tegula, fore and mid legs except coxae, hind trochanter, hind tarsus. Brown: flagellomeres except as indicated above, hind leg except trochanter and tarsus.

Female. Length 3.7–4.6 mm. Similar to male except as follows: apicoventral mandibular tooth enlarged, truncate, much larger than other teeth. Clypeal apex quadridentate as follows: lateral lobe flanking lateral edge of labrum, pair of smaller median teeth separated from lateral lobe by broad emargination and from each other by narrow U-shaped notch. Clypeal apex with specialized, elongate, flattened setae present on median teeth (2 per tooth) and on lateral lobe (6–7 per lobe) with occasionally single seta on emarginate interspace. Clypeus shiny, sparsely punctate, area immediately above median teeth impunctate and area between antennal sockets most densely punctate with punctures 1 diameter or less apart (elsewhere punctures 3 or more diameters apart). Lateral lobe yellow-brown to red-brown.

Material Examined (8♂, 16♀).—Holotype: ♂, PERU: Samne, ca. 40km ne. Trujillo, Prov. La Libertad 7°59's 78°41'w elev. ca. 1500m 12–17-VII-1975 C. Porter, L. Stange (LILLO). Paratypes: PERU: San Bartolome VII-1913 C.T. Brues (♂: 1 MCZ). **La Libertad:** same data as holotype (♂: 1 LILLO, 1 PMA). 15km e. Laredo 19-VII-1982 R.B. Miller, L. A. Stange (♂: 1

FSCA). **Lima:** Chancay shrubs nr. river 40 miles n. of Lima 29-VII-1971 P.S. & H.L. Broomfield B.M.1971–486 fertile irrigated region in arid coastal desert (♂: 1 BMNH). Chosica XI-1961 N.L.H. Krauss (♀ 1 USNM). Cupiche, 10km n. Chosica 25-VI-2-VII-1974 C. Porter & L. Stange (♂: 1 LILLO, ♀: 2 LILLO). Cupiche 26-VI-1976 C. Porter, C. Calmbacher (♂: 1 FSCA). Lima 13-XI-1950 E.S. Ross (♀: 2 CAS). Lima City, S. Marcos Univ. campus 26–27-IV-1983 Mal. trap C. & M. Vardy B.M.1983–217 (♀: 4 BMNH, 1 PMA). San Geronimo ca. Chosica 1–5-VII-1976 C. Porter, C. Calmbacher (♀: 3 FSCA). San Geronimo 30-VII-1982 R.B. Miller, L.A. Stange (♀: 2 FSCA). **VENEZUELA: Distrito Federal:** nr. Caracas 28-VIII-1943 D.G. Hall (♀: 1 USNM).

Distribution (Map 28).—Venezuela, Ecuador, Peru.

10. *Llaqhastigmus nigricollaris*

Finnamore, new species

Derivation of Name.—The species epithet is derived from two latin words, niger and collaris, in reference to the dark pronotal collar characteristic of this species.

Diagnosis.—The combination of a brown or black pronotal lobe, antennal scape yellow-brown and in the female the apico-dorsal mandibular tooth (in addition to apicoventral tooth) enlarged and truncate, will separate this species from all others in the genus.

Description.—Male. Length 3.7–3.9 mm.

Head. Sculpture of clypeus obscured by dense appressed setae. Gena ventrally, with sparse straight setae that are subequal to or less than greatest width of fore basitarsus. Microsculpture of frons more dense than that of vertex adjacent to mid ocellus. Occipital carina ventrally, raised and foveolate.

Mesosoma. Transverse sulcus of pronotum with longitudinal carinae. Scutum shiny, weakly microsculptured especially on disc, punctures sparse. Transscutellar sulcus foveolate. Preomalar area sparsely

setose, setae not obscuring underlying sculpture. Subomaulus present. Scrobal sulcus weakly impressed, irregularly foveolate anteriorly, occasionally entirely foveolate. Sternopleural region weakly microsculptured with sparse punctures and setae. Propodeum shiny, with several coarse areolae adjacent to enclosure composed of relatively high carinae.

Metasoma. Petiole with 2 to 4 coarse carinae laterally.

Color. Ground color black. Yellow to yellow-brown: palpi, mandibles medially, scape, pedicel and basal flagellomeres ventrally, tegula, fore and mid legs except coxae and usually except femora, hind trochanter and tarsus. Brown: mandible basally, antenna other than noted above, pronotal lobe, femora, hind tibia.

Female. Length 4.2–5.0 mm. Similar to male, except as follows: apicoventral and apicodorsal mandibular teeth enlarged, truncate. Clypeal apex quadridentate as follows: lateral lobe flanking lateral edge of labrum, pair of small median teeth separated from lateral lobe by deep, broad, emargination and from each other by shallow notch. Clypeal apex with specialized, flattened, elongate setae on lateral lobe (4 or 5) and on median teeth (2 per tooth) but generally absent on emarginate interspaces. Clypeus shiny, microsculpture absent, punctures sparse (3 or more diameters apart laterally, slightly more dense medially), lateral lobe red-brown.

Material Examined (2♂, 16♀).—Holotype: ♀, COLOMBIA: Valle Dept.: Penas Blancas 1750m 10km w. Cali, very wet premontane forest, R.C. Wilkerson 15-I-1975 Malaise trap (FSCA). Paratypes: COLOMBIA: **Cauca**: Popayan 1,800m 11-X-1974 M. Cooper B.M.1975–33 (1♂: 1 BMNH, ♀: 1 BMNH). **Valle**: Cali 900m 17-I-1972 M. Cooper B.M.1972–275 (♀: 1 BMNH). Pance CVC 1700m 15km w. Cali, very wet premontane forest, R.C. Wilkerson 23-XII-1974 Malaise trap (♀: 1 FSCA). Penas Blancas 1750m 10km w. Cali, very wet premontane forest, R.C. Wilkerson 23-

XII-1974 Malaise trap (♀: 1 FSCA). Penas Blancas 1750m 10km w. Cali, very wet premontane forest, R.C. Wilkerson 20–22-I-1975 Malaise trap (♀: 3 FSCA). Penas Blancas 1750m 10km w. Cali, very wet premontane forest, R.C. Wilkerson 31-I-1975 Malaise trap (♀: 3 FSCA, 1 PMA). Penas Blancas 12-II-1975 R. Wilkerson Malaise trap (♀: 3 FSCA, 1 PMA). Penas Blancas 17–19-III-1975 R. Wilkerson Malaise trap (♀: 1 FSCA). **ECUADOR: Napo**: El Chaco 2000m II-1983 M. Sharkey, L. Masner (♂: 1 BRD). **PERU: Huanuco**: Tingo Maria, 40 mi. s. Carpath Mts. XII-28–1954 E.I. Schlinger & E.S. Ross (♀: 1 CAS).

Distribution (Map 29).—Colombia, Ecuador, Peru.

11. *Llaqhastigmus santanderanus* Finnamore, new species

Derivation of Name.—The species epithet is derived from the Colombian state of Santander Del Norte, the northernmost record of the species.

Diagnosis.—The species is distinguished by the lack of a subomaulus, and a petiole that is finely carinate to microcarinate laterally. This species may prove to be conspecific with *australis*, at present there are too few specimens to assess variation within either species.

Description.—Male. Length 4.8–5.2 mm.

Head. Sculpture of clypeus obscured by dense appressed setae. Gena ventrally, with sparse straight setae that are subequal to or less than greatest width of fore basitarsus. Microsculpture of frons only slightly more dense than that of vertex. Occipital carina ventrally, raised and foveolate.

Mesosoma. Transverse sulcus of pronotum with longitudinal carinae. Scutum microsculptured, punctures sparse, obscure. Transscutellar sulcus not, or at most obscurely foveolate. Preomalar area sparsely setose, setae not obscuring underlying sculpture. Subomaulus absent. Scrobal sulcus slightly impressed, foveae absent or slightly evident anteriorly. Ster-

nopleural region microsculptured, sparsely punctate. Propodeum microsculptured, area adjacent to enclosure with fine irregular carinae, some small areolae dorsolaterally that are composed of fine, low carinae.

Metasoma. Petiole microcarinate laterally or with fine carinae laterally.

Color. Ground color black. White: mandible except apically, pronotal lobe. Yellow-brown: palpi, antenna, tegula, fore and mid legs except coxae, hind trochanter and tarsus. Brown: hind femur and tibia.

Female. Unknown.

Material Examined (2♂).—Holotype ♂, ECUADOR: Napo: Pastaza, Sebundoj, 2600m 11-15-IX-1977 L. Peña B.M.1978-293 (BMNH). Paratype: **COLOMBIA: Santander Del Norte:** Oroque 10-VI-1965 J.&B. Bechyne (♂: 1 UCV).

Distribution (Map 30).—Colombia, Ecuador.

12. *Llaqhastigmus sapanis* Finnamore, new species

Derivation of Name.—The species epithet is derived from the Quechua "sapan" meaning lone, in reference to the single known male specimen.

Diagnosis.—This species can be separated from all others in the genus with the following combination of characters: transverse sulcus of pronotum smooth and propodeum areolate dorsolaterally. The only other species known to have a smooth pronotal sulcus is *llutani* which differs from *sapanis* in its non-areolate propodeum.

Description.—Male. Length 3.8 mm.

Head. Sculpture of clypeus obscured by dense appressed setae. Gena ventrally, with sparse straight setae that are subequal to or less than greatest width of fore basitarsus. Microsculpture of frons more dense than that of vertex. Occipital carina ventrally, raised and foveolate.

Mesosoma. Transverse sulcus of pronotum smooth, without carinae. Scutum

microsculptured, punctures relatively coarse and sparse (usually 3 or more diameters apart on disc). Transscutellar sulcus foveolate. Preomalar area sparsely setose, setae not obscuring underlying sculpture. Subomalar present. Scrobal sulcus weakly impressed, not foveolate. Sternopleural region microsculptured, punctures sparse and evanescent. Propodeum microsculptured, area adjacent to enclosure and dorsolateral region areolate, areolae composed of relatively low carinae; side irregularly carinate.

Metasoma. Petiole carinate laterally.

Color. Ground color black. White: mandible except apically, pronotal lobe. Yellow-brown: palpi, scape, ventrally on pedicel and basal flagellomeres, tegula, fore and mid legs except coxae and femora, hind tarsus. Brown: antenna except as noted, fore and mid femora, hind leg except tarsus and coxa.

Female. Length 4.0–4.1 mm. Similar to male except as follows: apicoventral mandibular tooth enlarged, truncate, much larger than other teeth. Clypeal apex quadridentate as follows: lateral tooth flanking lateral edge of labrum, pair of smaller median teeth separated from lateral tooth by broad emargination and separated from each other by narrow U-shaped notch. Clypeal apex with specialized, flattened, elongate setae confined to teeth (2 per median tooth and 3 or 4 per lateral tooth). Clypeus shiny, without microsculpture, punctures sparse and relatively more dense between antennal sockets. Apical margin of clypeus black.

Material Examined (1♂, 4♀).—Holotype ♀, PERU: Machu Picchu XI-28-1965 H.& M. Townes (AEI). Paratypes: **BOLIVIA: Cochabamba:** Carrasco, Empalme 3000m II-1971 Fritz y Martinez (♂: 1 IIES). **PERU: Cuzco:** Machu Picchu XII-1-1965 H. & M. Townes (♀: 1 AEI). Machu Picchu II-24-27-1968 A. Garcia & C. Porter (♀: 2 MCZ).

Distribution (Map 31).—Bolivia, Peru.

13. **Llaqhastigmus shachus** Finnamore,
new species

Derivation of Name.—The species epithet is derived from the Quechua "sh'achu", meaning hairy in reference to the dense pilosity of this species.

Diagnosis.—This species can be distinguished by the presence of dense, elongate setae on the lower gena and sternopleural region. In the male, setae of lower gena are bent apically; in the female only a few near the hypostomal carina are bent apically. In both sexes the lower genal setae are longer than the greatest width of the fore basitarsus. Females of this species have a quadridentate mandible due to a deep U-shaped notch in the apicodorsal mandibular tooth (visible only by spreading the mandibles). All other species have tridentate mandibles and short sparse setae on the lower genal region. Setae in other species are never longer than greatest width of fore basitarsus. Other species have little or no setae on the sternopleural region.

Description.—Male. Length 4.4 mm.

Head. Sculpture of clypeus obscured by dense appressed setae. Gena ventrally, with dense elongate setae that are about twice the greatest width of fore basitarsus and bent 90° inward toward oral cavity. Microsculpture of frons slightly more dense than that of vertex. Occipital carina ventrally, raised and foveolate.

Mesosoma. Transverse pronotal sulcus carinate. Scutum microsculptured, punctures small and sparse. Transscutellar sulcus foveolate. Subomaulus present. Preomaular area densely setose, setae erect not obscuring underlying sculpture. Scrobal sulcus weakly impressed, a few evanescent irregular foveae anteriorly. Sternopleural region weakly microsculptured, densely and minutely punctate (punctures about 2 diameters apart ventrally); setae dense ventrally and elongate, slightly shorter than genal setae and with many tips bent 90° toward posterior. Propodeum

weakly microsculptured, area adjacent to enclosure and dorsolateral sphere with numerous areolae composed of relatively low carinae, side more or less vertically carinate with carinae merging into areolae of dorsolateral sphere.

Metasoma. Petiole laterally, with 4 longitudinal coarse carinae.

Color. Ground color black. White: mandibles basally, pronotal lobe. Yellow-brown: Palpi, mandible medially, scape ventrally, tegula, fore and mid legs except coxae and femora, hind tarsus.

Female. Length 4.8–5.4 mm. Similar to male except as follows: mandible quadridentate, apicodorsal tooth with deep U-shaped notch thereby imparting quadridentate appearance to the mandible; apicoventral mandibular tooth enlarged, truncate, much larger than other teeth. Clypeal apex quadridentate as follows: lateral lobe flanking lateral edge of labrum, pair of median teeth separated from lateral lobe by broad emargination and from each other by U-shaped notch. Clypeal apex with specialized, flattened, elongate setae distributed over most of apex. Clypeus shiny, without microsculpture, punctures sparse (5–10 diameters apart). Apical clypeal margin black. Genal and sternopleural setae not as dense or as long as those in male. Omaulus ending ventrally, not continued forward to acetabular carina.

Material Examined (1♂, 2♀).—Holotype: ♀, PERU: Huanuco IX-16–1954 E.I. Schlinger & E.S. Ross (CAS). Paratypes: **ECUADOR: Loja:** 14km w. Catamayo 1770m 9-VII-1989 L. Stange & R. Miller (♀: 1 FSCA). **PERU: Huánuco:** Huánuco IX-16–1954 E.I. Schlinger & E.S. Ross (♂: 1 CAS).

Distribution (Map 32).—Ecuador, Peru.

14. **Llaqhastigmus sharkeyi** Finnamore,
new species

Derivation of Name.—This species is named in honour of Michael J. Sharkey, co-collector of the primary type material.

Diagnosis.—The combination of a white

pronotal lobe; shiny scutum with punctures minute and sparse, without microsculpture on posterior $\frac{2}{3}$ except narrow posterior margin; and a coarsely foveolate scrobal sulcus will separate this species from all others in the genus.

Description.—Male. Length 3.6–4.7 mm.

Head. Sculpture of clypeus obscured by dense appressed setae. Gena ventrally, with sparse straight setae that are subequal to or less than greatest width of fore basitarsus. Microsculpture of frons more dense than that of vertex. Occipital carina ventrally, raised and foveolate.

Mesosoma. Transverse pronotal sulcus with longitudinal carinae. Scutum shiny on most of posterior $\frac{2}{3}$, microsculptured anteriorly and narrowly on posterior margin; punctures minute, sparse, 10 or more diameters apart. Transscutellar sulcus foveolate. Preomalar area sparsely setose, setae not obscuring underlying sculpture. Subomalar present. Scrobal sulcus impressed, foveolate. Sternopleural region shiny, without microsculpture, punctures minute and sparse. Propodeum shiny, without microsculpture, area adjacent to enclosure and lateral sphere with areolae composed of relatively high carinae; side unsculptured toward metapleuron.

Metasoma. Petiole carinate laterally.

Color. Ground color black. White: pronotal lobe. Yellow to yellow-brown: palpi, mandible medially, scape, pedicel, ventrally on basal flagellomeres or more, tegula, fore and mid legs except coxae, hind tarsus. Brown: antennal flagellum except as noted above, hind leg except tarsus.

Female. Length 4.2–4.6. Similar to male except as follows: apicoventral mandibular tooth enlarged, truncate, much larger than other teeth. Clypeal apex quadridentate as follows: lateral tooth flanking lateral edge of labrum, pair of smaller median teeth separated from lateral tooth by broad emargination and separated from each other by narrow U-shaped notch. Clypeal apex with 5 or 6 specialized, elongate, flattened setae equally distributed

along edge except for median teeth which bear 2 additional setae each. Clypeus shiny, punctures minute but dense laterally and larger and more sparse medially (1 to 2 diameters apart). Apical margin of clypeus black.

Material Examined (4♂, 4♀).—Holotype: ♂, ECUADOR: Napo Prov.: Baeza, 5km s. II-1983 2000m Sharkey, Masner (BRD). Paratypes: **COLOMBIA: Santander del Norte**: Prima 1700m 27-V-1965 J. & B. Bechyne (♀: 1 UCV). **ECUADOR: Napo**: Baeza, 5km s. II-1983 2000m Sharkey, Masner (♀: 1 BRD). El Chaco 2000m II-1983 M. Sharkey, L. Masner (♂: 1 PMA). Pastaza, Reventador 1750m 3–5-X-1977 L.E. Peña B.M.1978–293 (♂: 1 BMNH). **VENEZUELA: Aragua**: Hac. Portapan 1700m 15-VIII-1969 J. & B. Bechyne (♀: 1 UCV). Rancho Grande 1100m 16-XI-1967 J. & B. Bechyne (♀: 1 UCV). Rancho Grande, Portachuelo 1100m 22-V-1981 J.A. Clavijo, J.L. Garcia (♂: 1 UCV). **Falcon**: Curimagua 1400m 1-XII-1971 J. & B. Bechyne (♀: 1 UCV).

Distribution (Map 33).—Ecuador, Colombia, Venezuela.

GENERIC RELATIONSHIPS

The following hypothesis of relationships of genera among the Stigmina is based on outgroup analysis of character state distribution. The characters listed below were polarized by outgroup analysis with the Spilomenina. Morphology is after Bohart and Menke (1976) unless otherwise indicated in introduction, only characters not sufficiently treated by those authors are explained in detail below. In the following analysis 0 denotes the plesiotypic state and 1 to 5 denote various apotypic expressions of a character and do not necessarily represent transition series. Data matrices for the Stigmina, Pemphredonina, Spilomenina, and Ammoplanina are presented in Tables I–IV respectively. A cladogram illustrating relationships is presented in Fig. 51. The cladogram is based

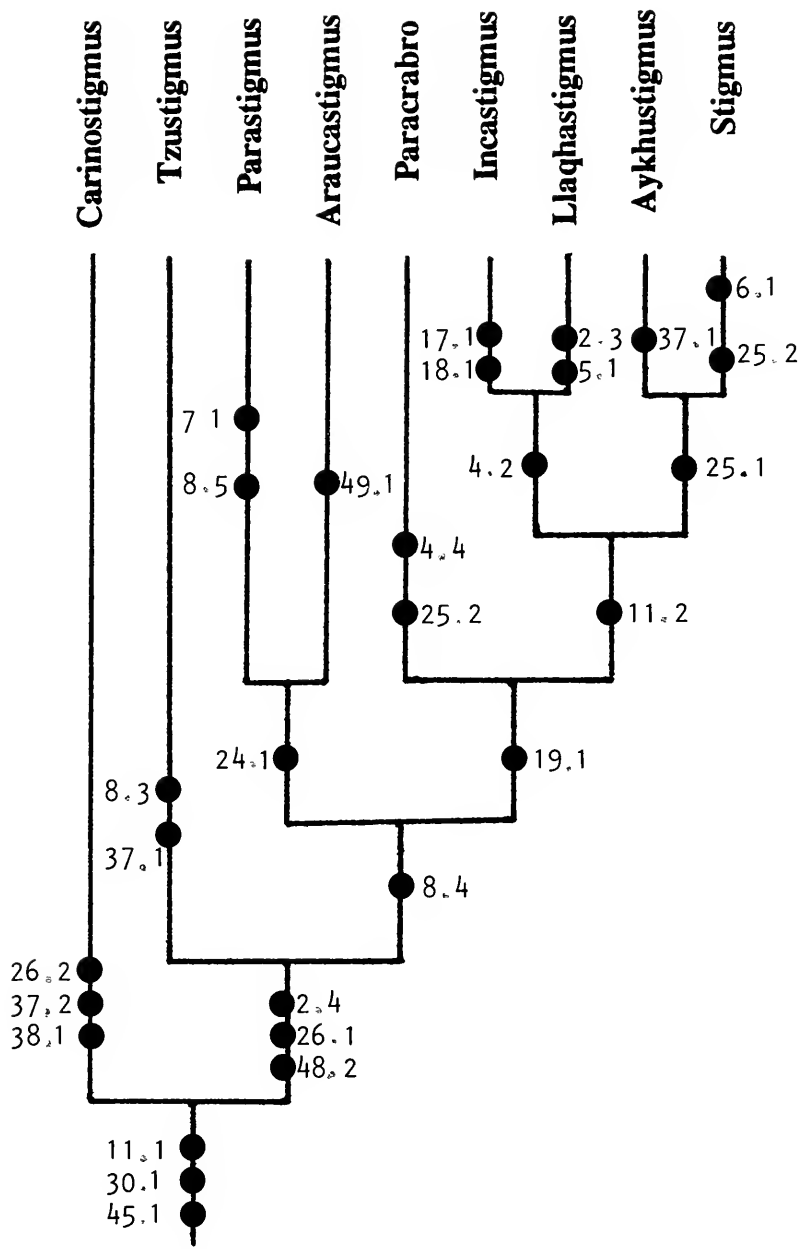


Fig. 51. Cladogram depicting relationships among genera of Stigmina.

on the following characters and was developed without electronic assistance.

Character Polarization

1. Palpal formula.

0—Palpal formula 6-4, palpal segments long, palpi conspicuous. Found in the

Stigmina and the Pemphredonina, palpal segment length generally exceeds twice its width, palpi greatly exceed hypostomal carina.

1—Palpal formula 6-4, palpal segments short, palpi inconspicuous. Found in the Ammoplanina (genera examined: *Pulver-*

ro, *Ammoplanus*, *Anmoplanops*, *Parammoplanus*, *Ammoplanellus*, *Timberlakena*), palpal segment length generally about twice its width or less, palpi at most slightly exceed hypostomal carina.

2—Palpal formula 5-4, palpal segments short, palpi inconspicuous. This character is synapomorphic for the Spilomenina and was the justification used by Menke (1989) to separate the group from the Stigmata. Palpal segments are short, particularly basal segments which may be no longer than wide, palpi at most slightly exceed hypostomal carina.

2. Labrum shape.

0—Labrum truncate to broadly rounded, wider than long. This character state is found in *Arpactophilus*, *Microstigmus*, *Xysma*, *Pulverro*, *Ammoplanops*, and many other apoid and vespoid wasps. This character state in the genera listed above may represent a reversal from 2.3 or 2.4. Only a few species and specimens were available for dissection in these groups, furthermore the difference between truncate and broadly rounded is sometimes slight, rendering the polarity of this character especially difficult to establish.

1—Labrum triangular, longer than wide. Present in *Pemphredon*, *Polemistus*, and *Carinostigmus*, as well as most Ampulicinae (*Ampulex*) and Ammophilini (Sphecinae). Sides of triangle are out-curved, basal and apical regions are not distinguished. This state may represent the correct plesiotypic expression of the labrum in the Pemphredonini.

2—Labial apex distinguished from base. In *Passaloecus* the lateral margins of the labrum are incurved resulting in a state in which the base is abruptly broadened and thereby distinguished from the apex. The abrupt shoulder is present, although modified, in all genera listed under 2.3, 2.4, and presumably 2.5 although I have not seen specimens of the latter.

3—Labrum emarginate to bilobed. This development ranging from a slight emar-

gination found in *Paracrabro* to the deeply bilobed expression found in *Diodontus*, *Llaqhastigmus*, *Arpactophilus*, *Ammoplanus*, *Parammoplanus*, *Anmoplanellus*, *Timberlakena* and as well is present in those genera listed under 2.4. The labrum of *Llaqhastigmus* is considered a character reversal from 2.4 caused by a reduction of the median lobes.

4—Labrum 4-lobed. This character state results from an apical shift of the lateral shoulders (see character state 2.2 above) imparting a 4-lobed appearance to the labrum. Found in *Stigmus*, *Tzustigmus*, *Arcaustigmus*, *Parastigmus*, *Aykhustigmus*, *Incastigmus*, *Arpactophilus*, and *Spilomena*.

5—Labrum 6-lobed. I have not seen specimens bearing this character. Menke (1989) noted undescribed *Arpactophilus* having a "six toothed labrum".

3. Mandibular socket.

0—Open.

1—Closed.

4. Apical mandibular teeth.

0—Mandible with 2 apical teeth. This character state is found in males of all genera of Stigmata, except *Incastigmus* and *Llaqhastigmus*, it also occurs in both sexes of all genera in the Spilomenina and sporadically in all genera of the Pemphredonina.

1—Mandible unidentate, apically terminating in a single point or truncate.

2—Mandible tridentate apically (Figs. 37, 39). Females of most genera of Stigmata (except *Parastigmus*, *Paracrabro* and some *Stigmus*) and males of *Incastigmus* and *Llaqhastigmus*. The character state also occurs in some species of *Passaloecus* and *Pemphredon*.

3—Mandible with 4 apical teeth.

4—Mandible with 5 apical teeth.

5—Mandible with 6 apical teeth.

5. Apicoventral mandibular tooth in females having a tridentate mandible (character 4.2).

0—Apicoventral tooth acute, similar in size to other teeth (Fig. 39).

1—Apicoventral tooth enlarged and truncate (Fig. 37). This character state occurs in females of *Llaqhastigmus* and independently in females of some *Pemphredon*.

6. Clypeal apicolateral bevel.

0—Clypeus unmodified apicolaterally.

1—Clypeal apex bevelled apicolaterally (Fig. 42). The lateral clypeal bevel is an autapotypic character state occurring in *Stigmus*. It occurs only in males and is most developed in species from the Neotropical Region.

7. Clypeus size.

0—Clypeus not reduced, antennal socket usually more than its diameter from nearest clypeal edge; labrum generally flat, lightly sclerotized, mostly or entirely obscured. Found in males and most females.

1—Clypeus reduced, antennal socket about its diameter from nearest clypeal edge, labrum convex, heavily sclerotized, entirely exposed, or almost so. Some females of a few genera.

8. Clypeal teeth.

0—Clypeus without teeth or lobes on apical margin.

1—Clypeus with single median tooth or lobe.

2—Clypeus with 2 median teeth.

3—Clypeus with 3 teeth.

4—Clypeus with 4 teeth.

5—Clypeus with 2 lateral teeth, median teeth lost.

9. Interantennal tubercle.

0—Reduced or absent, usually represented by a small, raised conical point, seldom exceeding half width of antennal scape (Fig. 36).

1—Protruberant, often exceeding width of antennal scape (Figs. 6, 7).

10. Frontal carina.

0—Frontal carina absent, indicated by a groove, complete or in part, from midocellus to clypeus.

1—Frontal carina absent, frons flat, without indication of groove or carina.

2—Frontal carina present as a simple raised line, complete or in part, from midocellus to ocellus.

3—Frontal carina strongly raised, lamellate, usually between antennal sockets.

11. Vertex micropore field.

0—Vertex, between lateral ocellus and eye, of similar microsculpture and punctation to adjacent areas; without group of loosely associated punctures or discrete pore field.

1—Vertex, between lateral ocellus and eye, with a loosely associated group of punctures (Figs. 3, 8).

2—Vertex, between lateral ocellus and compound eye, with a micropore field, appearing as a discrete patch of fine microsculpture relative to adjacent microsculpture (Figs. 19, 20, 25, 26, 31, 32).

12. Eye margins.

0—Eye not margined by a carina.

1—Eye at least partially margined by a carina.

13. Occipital Carina.

0—Occipital carina present, simple.

1—Occipital carina raised, foveolate.

2—Occipital carina incomplete dorsally, present ventrolaterally.

3—Occipital carina absent.

14. Occipital-hypostomal carinae.

0—Occipital carina intersecting hypostomal carina.

1—Occipital carina ending ventrally not intersecting hypostomal carina.

2—Occipital carina forming a complete circle, not intersecting hypostomal carina.

15. Pronotal collar.

0—Pronotal collar of normal length, transverse sulcus without median longitudinal raised area (Figs. 7, 10).

1—pronotal collar elongate, transverse sulcus with median longitudinal area raised (Figs. 2, 5).

16. Transverse pronotal carina.

0—Present, at least laterally.

1—Absent.

17. Median scutal groove.

0—Scutum without median groove or pit (Figs. 38, 41).

1—Scutum with a median groove or at least a median posterior pit (Figs. 33, 35).

18. Notaular grooves.

0—Notaular grooves unmodified, present anterolaterally (Figs. 38, 41).

1—Notaular grooves elongate, often to posterior margin of scutum (Figs. 33, 35).

19. Acetabular carina.

0—Acetabular carina absent (Fig. 11).

1—Acetabular carina present (Fig. 43).

20. Omaulus.

0—Omaulus present.

1—Omaulus absent.

21. Episternal sulcus.

0—Episternal sulcus present.

1—Episternal sulcus absent.

22. Hypersternaulus.

0—Hypersternaulus present.

1—Hypersternaulus absent.

23. Orientation of hypersternaulus.

0—Obliquely oriented.

1—Horizontally oriented.

24. Scrobal sulcus.

0—Present (Fig. 34).

1—Absent (Fig. 14).

25. ♂ midbasitarsus.

0—Midbasitarsus elongate, longer than remaining tarsomeres combined.

1—Midbasitarsus, straight, cylindrical, shorter than remaining tarsomeres combined.

2—Midbasitarsus short, modified—curved, excavated, expanded or combinations thereof.

26. Hindtibial spines.

0—One or more rows of spines on posterior surface.

1—2–4 widely separated spines on posterior surface.

2—Without spines on posterior surface.

27. Propodeal enclosure.

0—Present.

1—Absent.

28. Stigma size.

0—Stigma of fore wing of normal size, smaller than marginal cell.

1—Stigma of fore wing enlarged about size of marginal cell or larger.

29. Stigma shape.

0—Stigma of fore wing broadly lenticular.

1—Stigma of fore wing subglobular.

30. Stigma micropore field.

0—Stigma of fore wing without micropore field, dorsal surface uninterrupted.

1—Stigma of fore wing with micropore field, appearing as a discrete circular or elliptical microsculpture patch interrupting dorsal surface (Figs. 46, 47).

31. Marginal cell size.

0—Marginal cell not reduced, larger than stigma.

1—Marginal cell reduced, smaller than stigma.

32. Marginal cell veins.

0—Marginal cell closed.

1—Marginal cell open.

33. Submarginal cells.

- 0—Two submarginal cells.
- 1—One submarginal cell.
- 2—Submarginal cells absent.

34. Submarginal cell position.

0—Outer veinlet of submarginal cell 1 out of line with outer veinlet of marginal and discoidal cells.

1—Outer veinlet of submarginal cell 1 in line with outer veinlet of marginal and discoidal cells.

35. Submarginal cell I veins.

- 0—Submarginal cell I closed.
- 1—Submarginal cell I open.

36. Discoidal cell number.

- 0—Fore wing with three discoidal cells.
- 1—Fore wing with two discoidal cells.
- 2—Fore wing with one discoidal cell.

37. Hind wing media divergence.

0—Hind wing media diverging before or at cu-a.

1—Hind wing media diverging just after cu-a.

2—Hind wing media diverging far after cu-a.

38. Hind wing submedian cell.

0—Hind wing submedian cell about half or more length of median cell.

1—Hind wing submedian cell about one third length of median cell.

39. Hind wing cells.

- 0—Closed cells present in hind wing.
- 1—Hind wing without closed cells.

40. Petiole length.

0—Petiole undeveloped, abdomen sessile.

1—Petiole developed, composed of sternum only, wider than long. Some *Microstigmus* approximate this character state but the apparent petiole is composed of both tergum and sternum.

2—Petiole developed, composed of sternum only, longer than wide.

41. Petiolar sculpture.

0—Petiole carinate—2 or more longitudinal carinae.

1—Petiole punctate.

2—Petiole smooth and round.

42. Sternum I carinae.

0—Metasomal sternum 1 without basal carinae.

1—Metasomal sternum 1 with single basal medial carina.

2—Metasomal sternum 1 with two basal median carinae.

43. Sternum 1 basal groove.

0—Metasomal sternum 1 basal transverse groove undeveloped.

1—Metasomal sternum 1 with a transverse groove or constriction just posterior to base.

44. Tergum 1 lateral carina.

0—Metasomal tergum 1 with a lateral carina.

1—Metasomal tergum 1 lateral carina absent.

45. Sternum 2 microsetal patches.

0—Metasomal sternum 2 without microsetal patches.

1—Metasomal sternum 2 with discrete microsetal patch laterally (Figs. 44, 45).

46. Pygidial Plate.

0—Pygidial plate present, broad.

1—Pygidial plate present, narrow, trough-like.

2—Pygidial plate absent.

47. Male Sternum 8.

0—Metasomal sternum 8 broad, not narrowed apically.

1—Metasomal sternum 8 triangular, gradually narrowed apically.

2—Metasomal sternum 8 narrowly triangular, base differentiated from apex.

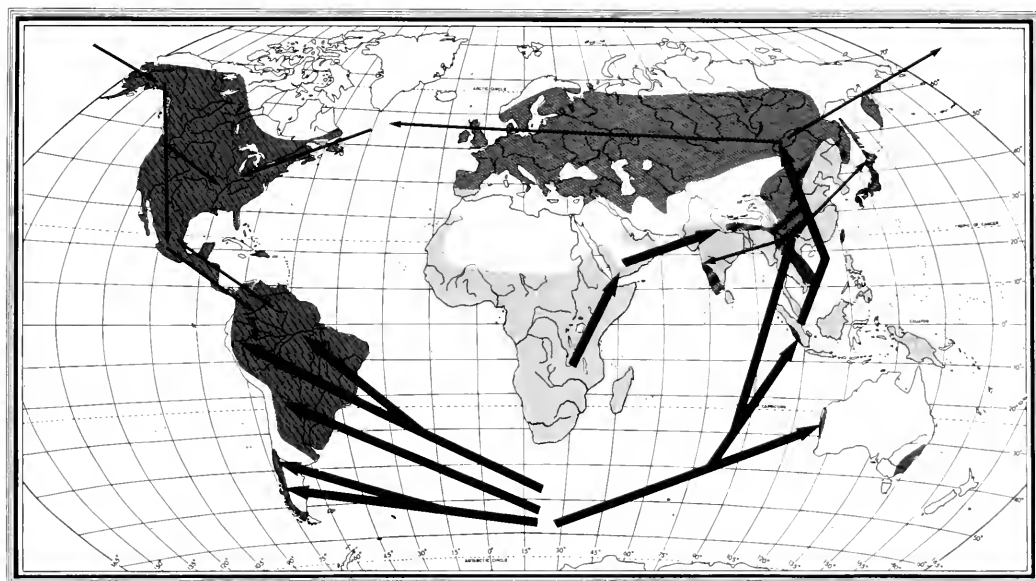


Fig. 52. World distribution and post continental drift dispersal routes for *Carinostigmus* (light shading) and other genera in the Stigmina (dark shading). Wide lines indicate generic level dispersals, narrow lines indicate species group dispersal.

3—Metasomal sternum 8 abruptly narrowed, apical portion forming a pseudosting, elongate and parallel-sided.

4—Metasomal sternum 8 spatulate apically.

48. Genitalia.

0—Digitus and cuspis lobular, more or less equal in length.

1—Digitus, elongate-triangular, longer than cuspis.

2—Digitus elongate, sides parallel, greatly exceeding cuspis.

49. Microsculpture.

0—Present on most of body, dull.

1—Absent, body shiny.

DISCUSSION

The relationship of subtribes within the Pemphredoninae remains the same as that presented in Bohart and Menke (1976). The sister subtribe to the Stigmina is presumed to be the Spilomenina, based on the shared presence of a 4-lobed labrum (character 2.4 above). The Ammoplanina

(synapotypies: loss of transverse pronotal carina 16.1 and loss of omaulus 20.1) is considered immediate outgroup to the Stigmina + Spilomenina based on the synapotypic presence of an enlarged fore wing stigma. The immediate outgroup to the Stigmina + Spilomenina + Ammoplanina is the Pemphredonina based on the synapotypic loss of the third submarginal cell and the presence of specialized setae on the apicomedial clypeal apex in females. The Pemphredoninae are in need of critical cladistic analysis.

In the Stigmina the analysis of characters resulted in three equally parsimonious solutions. Electronic analysis of the data would have undoubtedly resulted in many more. The cladogram (Figure 51) was selected on the basis of the best fit with plate tectonics. The recognition of new genera was based on the cladistic analysis coupled with biogeography and morphology. Morphological distinctions for genera are consistent with those for genera in Bohart and Menke (1976). A dendrogram placing *Paracrabro* in a posi-

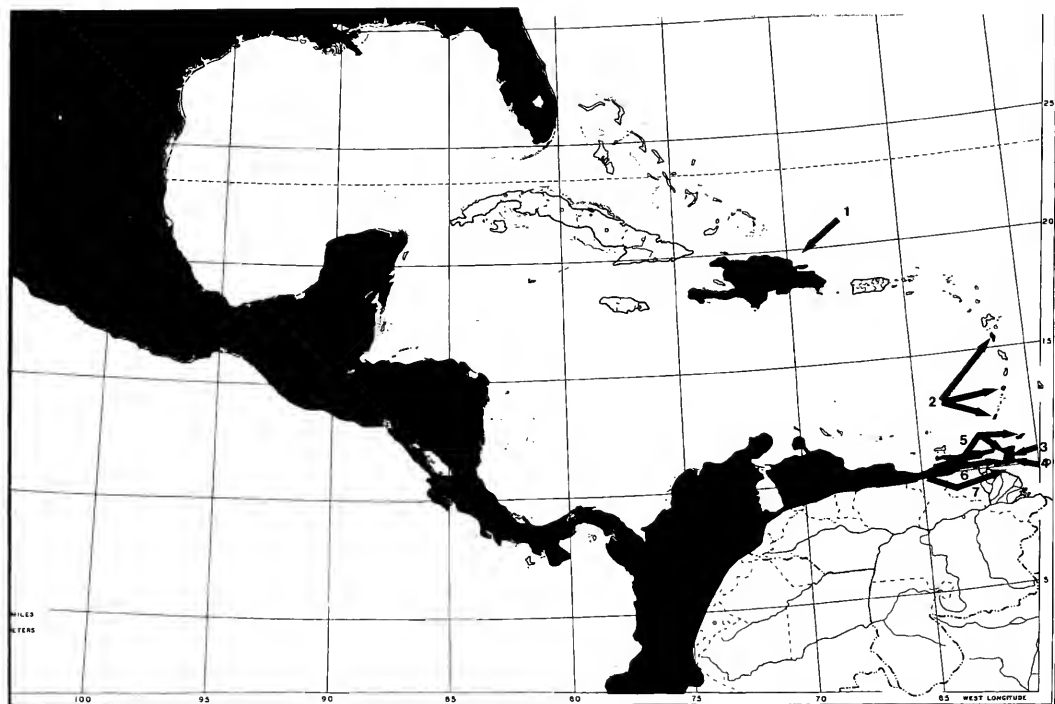


Fig. 53. Distribution of 27 species of *Stigmina* in the Caribbean.

tion basal to *Carinostigmus* and *Stigmus* was presented by Bohart and Menke (1976). The presence of a number of apotypic character states suggest that the arrangement presented here with *Carinostigmus* in the basal position, is correct. These character states include the presence of an acetabular carina, a clypeus with four teeth on the apical margin, two to four spines on the posterior surface of the hind tibia, and an elongate digitus that greatly exceeds the length of the cuspis.

A composite distribution map of the *Stigmina* is presented in Fig. 52, *Carinostigmus* is plotted against all other genera in the *Stigmina*. The presence of genera on two southern hemisphere continents and their absence on other continents is indicative of a group radiating at the time of continental separation. *Carinostigmus* is restricted to the Old World, generally southern hemisphere (based on large numbers of undescribed species from southern regions) but is absent from Australia (an

introduced species is present in New Guinea). The other genera occur in the western hemisphere (*Araucastigmus*, *Aykhustigmus*, *Incastigmus*, *Llaqhastigmus*, *Parastigmus*, *Stigmus*), across the Palaearctic Region with several outliers on the east asian islands and the orient (*Stigmus*, *Tzustigmus*), and Australia (*Paracrabro*). The only major zone of contact between *Carinostigmus* and the other genera is in the Oriental Region; a minor contact zone occurs in southern Spain. Elsewhere *Carinostigmus* is separated from the other genera by the Himalayas, the Gobi and Sahara Deserts, and the Atlantic Ocean.

Outliers in Chile, India, Thailand, Japan, Taiwan, Vietnam, Sumatra and Australia represent distributions of relict genera and species. The only anomaly is the presence of *Carinostigmus* in New Guinea which probably represents a recent introduction. The *Stigmina* are restricted in distribution by 2 primary barriers, those of xeric conditions and water. The effect of xeric con-

ditions is evident in Fig. 52 with the absence of genera from major desert regions (some exceptions in the New World). The effect of water is evident in the Caribbean fauna (Fig. 53). This composite distribution map of 27 species shows only 7 species on the Caribbean Islands, of those six occur within the area influenced by the Orinoco River current where 3 are endemic (including *Incastigmus thoracicus*). A fourth endemic species (an undescribed *Stigmus*) occurs on Hispaniola. Many of the islands of the Lesser Antilles are within sight of neighbouring islands. The failure of the Stigmina to traverse these short distances is indicative of the effectiveness of water as a barrier to dispersal and also to the lack of long distance dispersal mechanisms within this group. This point must be born in mind when attempting to interpret the present distribution patterns of genera. If there was not, at some time in the past, an overland route between points presently separated by water, then it is unlikely that species of Stigmina would disperse between those points.

In South America *Stigmus* has a C-shaped distribution restricted to the highlands surrounding the Amazon basin and restricted by the lowlands of the Río Pirana in the south. *Araucastigmus* (Map 35) is restricted to Chile, for the most part to the Pacific side of the continental divide and to the north restricted by extreme desert conditions. There are 3 species, and thanks to Lubomir Masner, an abundance of specimens. *Parastigmus* (Map 34) occurs on the east side of the divide although 1 species, the most plesiotypic in the genus occurs in Chile, possibly indicating a common regional origin. In Argentina *Parastigmus* appears to follow the distribution of grassy steppe vegetation surrounding the xeric vegetation of Patagonia. The genus is represented by 4 species known from 16 specimens. *Aykhustigmus* (Map 36), represented by 4 species known from 37 specimens, occurs in the Brazilian Highlands south to the Río Pirana and the

15.5°C mean July isotherm. The only exception is a single specimen recently collected from the Venezuelan state of Zulia believed to be an introduction. *Llaqhastigmus* (Map 37) follows a distribution similar to but not as extensive as *Stigmus*. Thirteen species are confined to the Andes while a single species occurs across the Brazilian Highlands. *Llaqhastigmus* is not known from the Guyana Shield but could well occur there. *Incastigmus* with 25 species is not only the largest Neotropical genus but has the broadest distribution. It is limited in the south by the 15.5°C mean July isotherm, on the west by xeric conditions and to the north by the 10°C mean January isotherm which is the approximate boundary of the Nearctic and Neotropical Regions. The composite map (Fig. 54) demonstrates the limiting influences of winter temperatures and rainfall on the distribution of Stigmina in the Neotropics.

About 200 million years ago a single landmass stretched from pole to pole, Laurasia to the north, Gondwanaland to the south. The central part of this great landmass was dominated by xeric conditions. Areas of rainforest existed in the extreme south (southern South America, South Africa, Antarctica and Australia), seasonal or monsoon rains existed in the mid latitudes (southeast Asia, Arabian Peninsula) (Lamb 1977). Superimposed on these extremes of wet-dry conditions were areas of exposed basement layer or granite shield characterized by localized or edaphic aridity (Axelrod 1972). Similar conditions occur today in the Tipui system of the Guiana Shield. The predrift uplifting of the continents along rift lines allowed water to flow east and west from the South American-African divide thereby slowly exposing the basement layer through erosion. The exposure of the basement layer in this region has probably had more consequences for floral and faunal radiation than any other single post drift event.

The Stigmina belong to the apoid lin-



Fig. 54. Composite distribution of *Incastigmus*, *Araucastigmus*, *Parastigmus* and *Aykhustigmus* in the Neotropical region.

eage (Apoidea) of Hymenoptera, of which bees form the dominant component. There is a well known coevolutionary relationship between bees and angiosperms. The earliest flowers were probably beetle pollinated (Michener 1979). Bees were probably an already diversified west gondwanan group of sandnesting lineages (Michener 1979) by the time the first flowering plants (Magnoliaceae) spread southward from Laurasia (Raven and Axelrod

1974). Michener (1979) for bees, and Axelrod (1972) and Raven and Axelrod (1974) for angiosperms hypothesize a xeric west Gondwanaland radiation of these groups. The influences of interior xeric conditions, thousands of island-like patches of arid exposed basement layer, along with a group of wasps (bees) preadapted for pollination contributed to an explosive radiation of bees and angiosperms.

Conversely the southern rainforests pre-

sented a habitat unsuitable for sand nesting organisms perhaps because of high water tables, high humidity and the likely persistence of fungi in brood cells. I hypothesize that twig-nesting behaviour developed early in the apoid lineages as a response to increasingly wet conditions to the south. It is also likely that twig-nesting developed more than once since there are several apparently unrelated types of aerial nest architecture. It is the twig nesting groups that reach the greatest diversity in the rainforests today. Lineages of bees, and the Stigmina likely radiated from one or the other of the two extreme gondwanaland ecosystems. Modern distributions show presumed relict bees inhabiting south temperate xeric areas while presumed relict Stigmina inhabit south wet temperate or tropical rainforest. Based on present-day distribution and on the hypothesized relationships between genera, the Stigmina probably existed prior to continental breakup, over 200 million years ago. Some support is lent to this statement by the existence of specialized pemphredonine fossils in the Upper Cretaceous, about 135 million B.P. (Evans 1969, 1973). Stigmina at the time of continental breakup would likely have occurred in the southern rainforests (southern South America, South Africa, Antarctica, Australia) and in the southern savanna surrounding the midcontinental xeric area.

Of pivotal importance in this analysis is a report on the tectonics of the Indonesian region (Hamilton 1979). Hamilton presents evidence of Jurassic (180 million B.P.) rifting of eastern Gondwanaland. Present-day land masses of Thailand, Burma, Malaysian Peninsula, Sumatra and Borneo rifted from the northern Australia–New Guinea–Antarctica continental margin and moved north to collide with the Eurasian plate. Furthermore Audley-Charles (1987) found an uninterrupted pollen record indicating the craton was not submerged during its northward jour-

ney and likely introduced Gondwanaland flora and fauna into Southeast Asia. If this tectonic event occurred, then gondwanaland flora and fauna (Stigmina) could be introduced to the Laurasian continent at a very early period. This would allow the lineages of Stigmina to be in a position to colonize the Nearctic Region via Europe and Beringia at 65 million B.P.

The rifting of South America from Africa commenced during the same period (180 million B.P.) and resulted in the separation of southern Africa from southern South America by a narrow body of water. The inability of the Stigmina to cross a water barrier is instrumental in my explanation of the absence of genera other than *Carinostigmus* from Africa. Although India likely once held more genera of Stigmina than it does today, that fauna was almost certainly lost when the craton travelled over a hot spot in the crust on its northward journey. Severe volcanism on the Indian plate likely caused extinction of biota in virtually all its ecosystems. What fauna the plate brought to Asia is probably the result of a brief encounter with north Africa before colliding with Asia about 45 million years B.P. By the late Cretaceous Period (135 million years B.P.) *Stigmus* and *Tzustigmus* probably colonized Laurasia. The Nearctic fauna consists of eastern and western species groups likely the result of colonization by *Stigmus* via both Europe and Beringia about 65 million years B.P.

Based on relationships presented in the cladogram and present distributions it is likely that the Stigmina originated in the southern hemisphere continents, especially Antarctica (Fig. 52) over 200 million years B.P. Australia was colonized once (*Paracrabro*). South America was colonized at a very early stage (180 million B.P.) on at least 3 separate occasions, and more recently by *Stigmus* from the Nearctic Region about 5 million B.P. North America was colonized at least twice, 3 times if one includes the incursion of Neotropical fau-

na (*Incastigmus*) into Central America about 5 million B.P. The Palaearctic was colonized at least twice; finally the Oriental Region was colonized on at least 2 occasions.

The great diversity of the Neotropical fauna is due to 3 major factors. The wet adapted fauna that colonized it, periodic aridity that likely restricted that fauna to islands of forest, and mountains that allowed extremes in climatic conditions to exist in close proximity. The xeric areas of southern Argentina afford the best opportunity to collect relict stigmene species in the New World.

By contrast the relatively depauperate nature of the Afrotropical fauna may be the result of a xerically adapted original fauna succumbing to the spread of mesic conditions over the entire continent, including the Sahara (Axelrod and Raven 1978). There was no, or very little, of the faunal island effect that occurred in South America. An increasingly wet Africa probably afforded little opportunity for the xerically adapted fauna to survive. Africa is again in a dry phase with rainforest restricted to very limited areas. The more equitable continental outliers such as the mesic islands of the Comoros or Madagascar probably still harbour remnants of relict faunas.

The interactions in the Oriental Region are complex. Most of the relict taxa are found there. Species of relict groups have highly localized distributions thus accounting for their relative absence in most collections. There is a possibility that their distributions are tied to forest over limestone terrain. Whitmore (1984) reported that limestone terrain is not common in Malaysia, but the flora of a mainland forest over limestone formation had 23% of its species endemic to the country with 11% endemic to limestone. Islands like Borneo or Sulawesi are melange formations (Hamilton 1979) resulting from nearby subduction zones indicating that limestone has likely been present throughout

the islands history. Although no habitat information is available for the relict fauna, it is likely, because of the high degree of endemic flora that limestone forest may offer fertile grounds for collecting specimens of these ancient apoid wasp lineages.

Little mention has been made of the origins of *Carinostigmus*. Two scenarios exist based on the cladogram, present distribution, and the number of undescribed species. In the first scenario I hypothesize an African origin with the genus in place at the time of rifting from South America or shortly thereafter. In the second scenario I hypothesize an Oriental origin with more recent colonization of Africa. The Oriental Region is a mix of land masses of Laurasian and Gondwanaland origin, and most species of *Carinostigmus* occur there (mostly undescribed). If a cladistic analysis of species within *Carinostigmus* were to demonstrate a Laurasian origin then the age of lineages in the Stigmata could be moved back to a Pangean origin about 230 million B.P. It would also imply a north-south Pangean split of lineages within the Stigmata with *Carinostigmus* of northern (Laurasian) origin and all other genera of southern origin (Gondwanaland). Such a scenario is compatible with the cladogram presented here and with ecosystem reconstructions of that period.

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Table 1. Data matrix for the Stigmata

| | Carino | Tzustig | Arauca | Parac | Parastig | Aykhys | Stigmus | Llaqh | Incast |
|------------------------------------|----------|----------|----------|----------|----------|----------|-------------|----------|----------|
| 1. Palpal formula | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2. Labrum shape | 1 | 4 | 4 | 4 | 4 | 4 | 4 | 3 | 4 |
| 3. Mandibular socket | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 4. Apical manibular teeth | 0♂ 2♀ | 0♂ 2♀ | 0♂ 2♀ | 0♂ 4♀ | 0♂ 0♀ | 0♂ 2♀ | 0♂ 0, 2♀ | 2♂ 2♀ | 2♂ 2♀ |
| 5. Apicoventral tooth | 0 | 0 | 0 | na | na | 0 | 0 | 1 | 0 |
| 6. Clypeal bevel | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| 7. Clypeus size | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| 8. Clypeal teeth | 2 | 3 | 4 | 5 | 4, 5 | 4 | 2, 4 | 4 | 4 |
| 9. Interantennal tubercle | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 10. Frontal carina | 2 | 0 | 2 | 2 | 0, 2 | 0 | 0 | 0 | 0 |
| 11. Vertex micropore field | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 |
| 12. Eye margins | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 |
| 13. Occipital carina | 0, 1 | 0, 1 | 0 | 1 | 0 | 0, 1 | 0, 1 | 0, 1 | 0, 1 |
| 14. Occi-hypo. carina | 2 | 2 | 2 | 2 | 2 | 2 | 1, 2 | 2 | 2 |
| 15. Pronotal collar | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 16. Transverse pronotal carina | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 17. Median scutal groove | 0, 1 | 0 | 0 | 0 | 0 | 0, 1 | 0 | 0 | 1 |
| 18. Notaular grooves | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 19. Acetabular carina | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 |
| 20. Omaulus | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 21. Episternal sulcus | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 22. Hypersternaulus | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 23. Orientation of hypersternaulus | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 24. Scrobal sulcus | 0, 1 | 0, 1 | 1 | 0 | 0, 1 | 0 | 0 | 0 | 0 |
| 25. ♂ midbasitarsus | 0 | 0 | 0 | 2 | 1 | 1 | 2 | 0 | 0 |
| 26. Hindtibial spines | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 27. Propodeal enclosure | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 28. Stigma size | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 29. Stigma shape | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 30. Stigma pore field | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 31. Marginal cell size | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 32. Marginal cell veins | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 33. Submarginal cells | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 34. Submarginal position | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 35. Submarginal veins | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 36. Discoidal cell number | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 37. Media divergence | 2 | 1 | 0 | 0 | 0 | 0, 1 | 0 | 0 | 0 |
| 38. Submedian cell | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 39. Hind wing cells | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 40. Petiole length | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 |
| 41. Petiolar sculpture | 2 | 0, 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 42. Sternum I carinae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 43. S1 basal groove | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 44. T1 lateral carina | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 45. S2 microsetae | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 46. Pygidial Plate | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 |
| 47. Male Sternum 8 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 |
| 48. Genitalia | 0 | 2 | 0 | 2 | 2 | 2 | 2 | 2 | 2 |
| 49. Microsculpture | 1 | 0, 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |

0 = plesiotypic character state, 1–6 = apotypic character states, na = not applicable, Carino = *Carinostigmus*, Tzustig = *Tzustigmus*, Arauca = *Araucastigmus*, Parac = *Paracrabro*, Parastig = *Parastigmus*, Aykhys = *Aykhustigmus*, Llaqh = *Llaqhastigmus*, Incast = *Incastigmus*.

Table 2. Data matrix for the Pemphredonina

| | <i>Diodontus</i> | <i>Pemphredon</i> | <i>Passaloecus</i> | <i>Polemistus</i> |
|------------------------------------|------------------|-------------------|--------------------|-------------------|
| 1. Palpal formula | 0 | 0 | 0 | 0 |
| 2. Labrum shape | 3 | 1 | 2 | 1 |
| 3. Mandibular socket | 1 | 1 | 1 | 1 |
| 4. Apical manibular teeth | 0, 1 | 2, 3, 4, 5 | 0, 2 | 0, 1 |
| 5. Apicoventral tooth | na | 0, 1 | 0 | na |
| 6. Clypeal bevel | 0 | 0 | 0 | 0 |
| 7. Clypeus size | 0 | 0 | 0 | 0 |
| 8. Clypeal teeth | 3 | 1, 2, 3 | 1, 2, 3 | 1 |
| 9. Interantennal tubercle | 0 | 0 | 0 | 1 |
| 10. Frontal carina | 2 | 2 | 0 | 2 |
| 11. Vertex micropore field | 0 | 0 | 0 | 0 |
| 12. Eye margins | 0 | 0 | 0 | 1 |
| 13. Occipital carina | 0 | 0 | 0 | 1 |
| 14. Occi.-hypo. carina | 1 | 1 | 2 | 2 |
| 15. Pronotal collar | 0 | 0 | 0 | 0 |
| 16. Transverse pronotal carina | 0 | 0 | 0 | 0 |
| 17. Median scutal groove | 0 | 0 | 0 | 0 |
| 18. Notaular grooves | 0 | 0 | 0 | 1 |
| 19. Acetabular carina | 0 | 0 | 0 | 0 |
| 20. Omaulus | 0 | 0 | 1 | 0 |
| 21. Episternal sulcus | 0 | 0 | 0 | 0 |
| 22. Hypersternaulus | 0 | 0 | 0 | 0 |
| 23. Orientation of hypersternaulus | 0 | 0 | 1 | 1 |
| 24. Scrobal sulcus | 0 | 0 | 0 | 0 |
| 25. ♂ midbasitarsus | 1 | 1 | 1 | 1 |
| 26. Hindtibial spines | 0 | 0 | 2 | 2 |
| 27. Propodeal enclosure | 0 | 0 | 1 | 0 |
| 28. Stigma size | 0 | 0 | 0 | 0 |
| 29. Stigma shape | 0 | 0 | 0 | 0 |
| 30. Stigma pore field | 0 | 0 | 0 | 0 |
| 31. Marginal cell size | 0 | 0 | 0 | 0 |
| 32. Marginal cell veins | 0 | 0 | 0 | 0 |
| 33. Submarginal cells | 0 | 0 | 0 | 0 |
| 34. Submarginal position | 0 | 0 | 0 | 0 |
| 35. Submarginal veins | 0 | 0 | 0 | 0 |
| 36. Discoidal cell number | 0 | 0 | 0 | 0 |
| 37. Media divergence | 0 | 0 | 0 | 0 |
| 38. Submedian cell | 0 | 0 | 0 | 0 |
| 39. Hind wing cells | 0 | 0 | 0 | 0 |
| 40. Petiole length | 1 | 2 | 1 | 2 |
| 41. Petiolar sculpture | 0 | 1 | 0 | 0 |
| 42. Sternum I carinae | 1 | 1 | 1 | 1 |
| 43. S1 basal groove | 0 | 0 | 0 | 0 |
| 44. T1 lateral carina | 0 | 0, 1 | 0 | 0 |
| 45. S2 microsetae | 0 | 0 | 0 | 0 |
| 46. Pygidial Plate | 0 | 1 | 2 | 2 |
| 47. Male Sternum 8 | 1 | 1 | 3 | 3 |
| 48. Genitalia | 0 | 0 | 0 | 0 |
| 49. Microsculpture | 0 | 0, 1 | 0 | 0 |

0 = plesiotypic character state, 1-6 = apotypic character states, na = not applicable.

Table 3. Data matrix for the Spilomenina

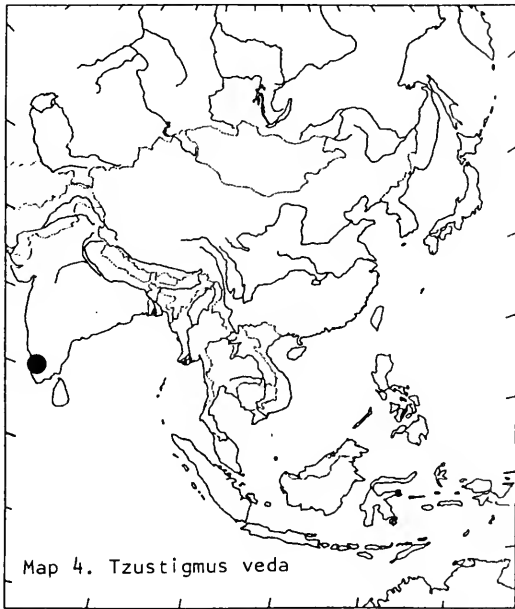
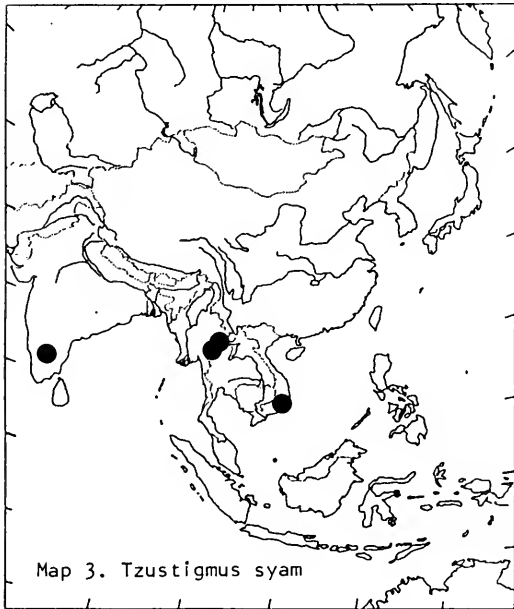
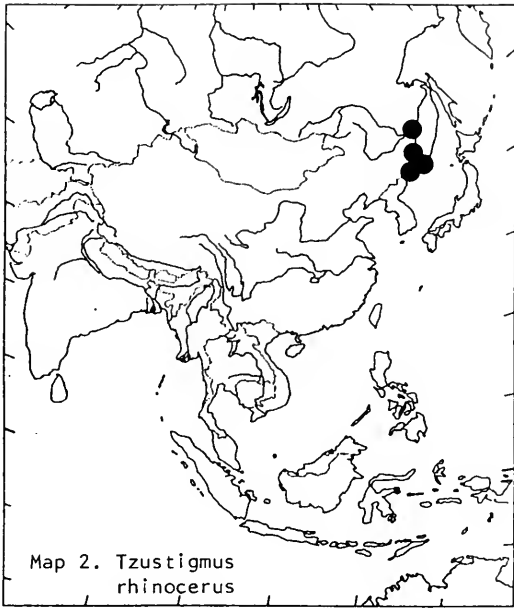
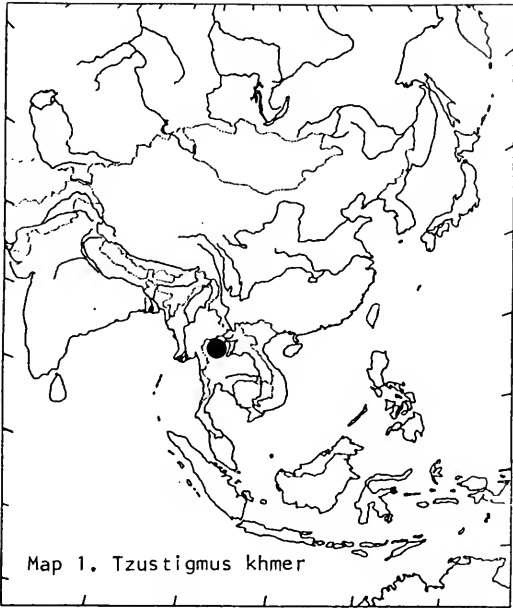
| | <i>Arpactophilus</i> | <i>Spilomena</i> | <i>Microstigmus</i> | <i>Xysma</i> |
|------------------------------------|----------------------|------------------|---------------------|--------------|
| 1. Palpal formula | 2 | 2 | 2 | 2 |
| 2. Labrum shape | 3, 4, 5 | 4 | 0? | 0? |
| 3. Mandibular socket | 1 | 1 | 1 | 1 |
| 4. Apical mandibular teeth | 0 | 0 | 0 | 0 |
| 5. Apicoventral tooth | na | na | na | na |
| 6. Clypeal bevel | 0 | 0 | 0 | 0 |
| 7. Clypeus size | 1 | 1 | 1 | 1 |
| 8. Clypeal teeth | 2 | 2 | 2 | 1 |
| 9. Interantennal tubercle | 0 | 0 | 0 | 0 |
| 10. Frontal carina | 2, 3 | 0, 1 | 2 | 2 |
| 11. Vertex micropore field | 0 | 0 | 0 | 0 |
| 12. Eye margins | 1 | 0 | 0 | 0 |
| 13. Occipital carina | 2 | 2, 3 | 3 | 3 |
| 14. Occi.-hypo. carina | 2 | na | na | na |
| 15. Pronotal collar | 0 | 0 | 0 | 0 |
| 16. Transverse pronotal carina | 0 | 0 | 0 | 0 |
| 17. Median scutal groove | 0 | 0 | 0 | 0 |
| 18. Notaular grooves | 0 | 0 | 0 | 0 |
| 19. Acetabular carina | 0 | 0 | 0 | 0 |
| 20. Omaulus | 0 | 0 | 0 | 0 |
| 21. Episternal sulcus | 1 | 1 | 1 | 1 |
| 22. Hypersternaulus | 0 | 0, 1 | 0 | 1 |
| 23. Orientation of hypersternaulus | 1 | 1 | 1 | na |
| 24. Scrobal sulcus | 0, 1 | 1 | 1 | 1 |
| 25. ♂ midbasitarsus | | 1 | | |
| 26. Hindtibial spines | 2 | 2 | 2 | 2 |
| 27. Propodeal enclosure | 1 | 0 | 1 | 1 |
| 28. Stigma size | 1 | 1 | 1 | 1 |
| 29. Stigma shape | 0 | 0 | 0 | 0 |
| 30. Stigma pore field | 0 | 0 | 0 | 0 |
| 31. Marginal cell size | 0 | 0 | 0 | 0 |
| 32. Marginal cell veins | 0 | 0 | 0 | 1 |
| 33. Submarginal cells | 0, 1 | 0 | 1 | 2 |
| 34. Submarginal position | 0 | 0 | 0 | 0 |
| 35. Submarginal veins | 0 | 0 | 0 | 1 |
| 36. Discoidal cell number | 1 | 1 | 1 | 2 |
| 37. Media divergence | 0 | 0 | 0 | na |
| 38. Submedian cell | 0 | 0 | 0 | na |
| 39. Hind wing cells | 0 | 0 | 0 | 1 |
| 40. Petiole length | 0 | 0 | 0 | 0 |
| 41. Petiolar sculpture | na | na | na | na |
| 42. Sternum I carinae | 2 | 2 | 2 | 2 |
| 43. S1 basal groove | 0 | 0 | 0 | 0 |
| 44. T1 lateral carina | 0 | 0 | 0 | 0 |
| 45. S2 microsetae | 0 | 0 | 0 | 0 |
| 46. Pygidial Plate | 2 | 2 | 2 | 2 |
| 47. Male Sternum 8 | | 2 | | |
| 48. Genitalia | | 1 | | |
| 49. Microsculpture | 0 | 0 | 0 | 0 |

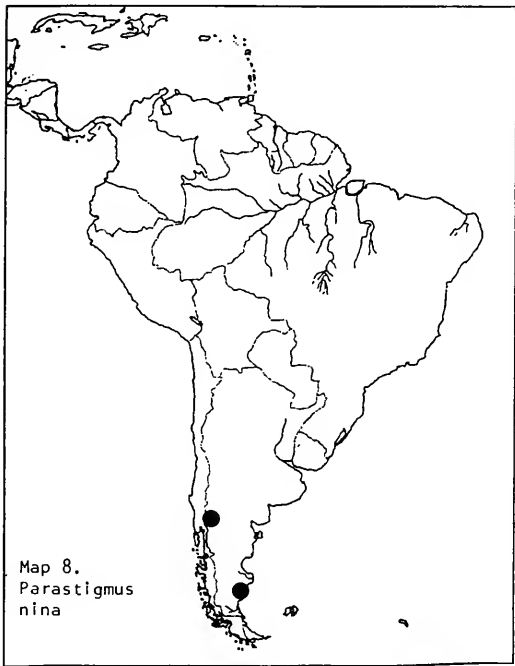
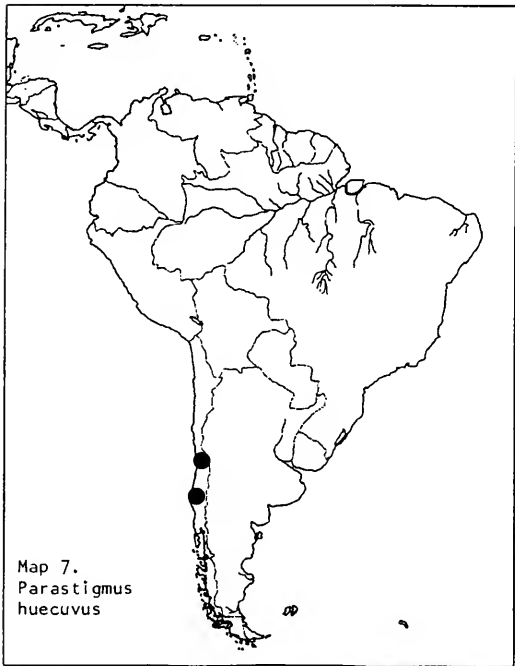
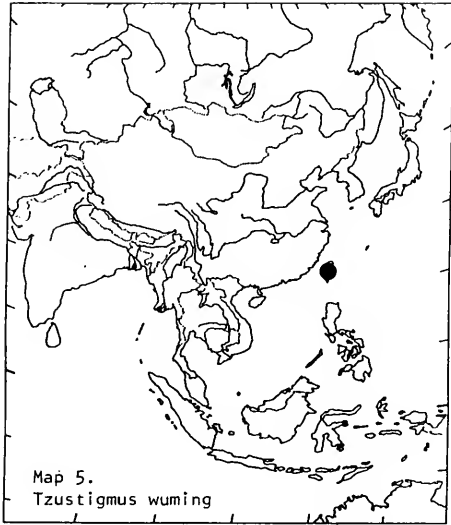
0 = plesiotypic character state, 1–6 = apotypic character states, na = not applicable, blank cells indicate specimens were unavailable and character state could not be determined from literature.

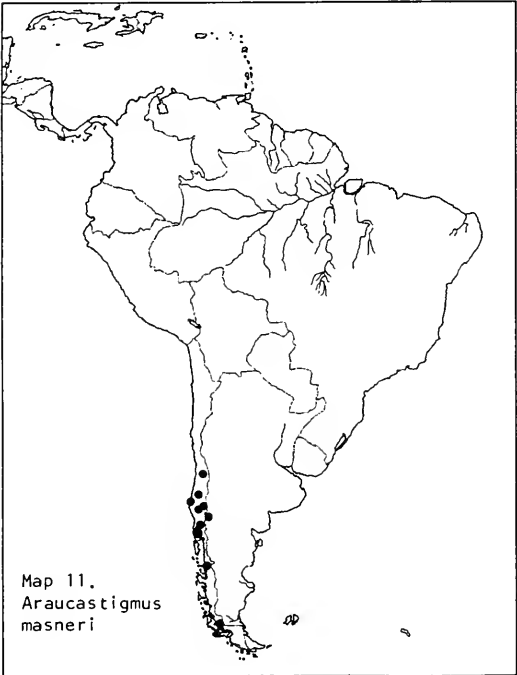
Table 4. Data matrix for the Ammoplanina

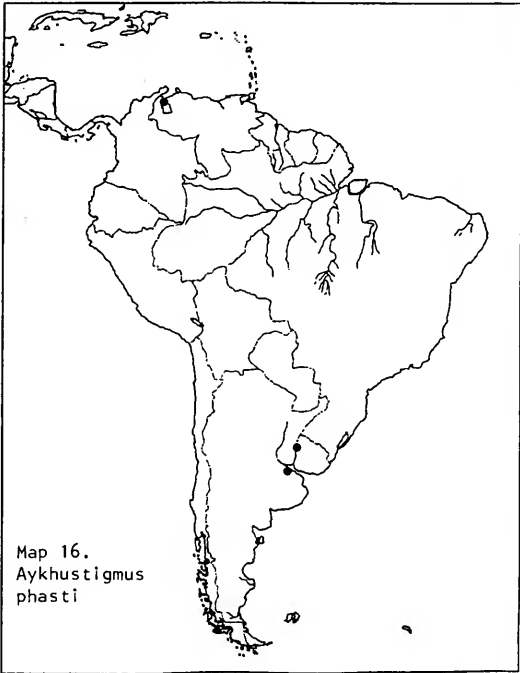
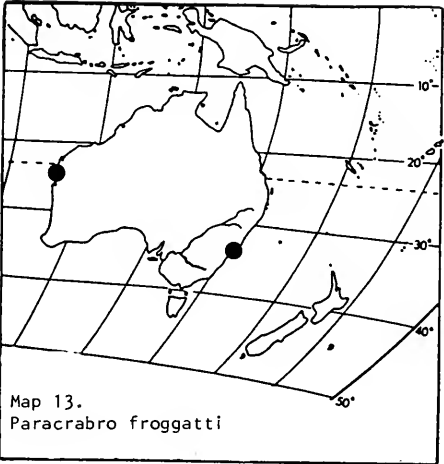
| | Pulv | Ammops | Ammous | Paramo | Ammoplus | Timber |
|------------------------------------|------|--------|--------|--------|----------|---------|
| 1. Palpal formula | 1 | 1 | 1 | 1 | 1 | 1 |
| 2. Labrum shape | 0? | 0? | 3 | 3 | 3 | 3 |
| 3. Mandibular socket | 1 | 1 | 1 | 1 | 1 | 1 |
| 4. Apical manibular teeth | 0 | 0 | 0 | 0 | 0 | 0 |
| 5. Apicoventral tooth | na | na | na | na | na | na |
| 6. Clypeal bevel | 0 | 0 | 0 | 0 | 0 | 0 |
| 7. Clypeus size | 0 | 0 | 1 | 1 | 1 | 1 |
| 8. Clypeal teeth | 2 | 2 | 2 | 2 | 2 | 2 |
| 9. Interantennal tubercle | 0 | 0 | 0 | 0 | 0 | 0 |
| 10. Frontal carina | 0, 1 | 1 | 0 | 1 | 0 | 1 |
| 11. Vertex micropore field | 0 | 0 | 0 | 0 | 0 | 0 |
| 12. Eye margins | 0 | 0 | 0 | 0 | 0 | 0 |
| 13. Occipital carina | 2 | 2 | 2 | 2 | 0 | 3 |
| 14. Occi.-hypo. carina | 2 | 1 | 1 | 1 | 1 | na |
| 15. Pronotal collar | 0 | 0 | 0 | 0 | 0 | 0 |
| 16. Transverse pronotal carina | 0 | 0, 1 | 1 | 1 | 1 | 1 |
| 17. Median scutal groove | 0 | 0 | 0 | 0 | 0 | 0 |
| 18. Notaular grooves | 0 | 0 | 0 | 0 | 0 | 0 |
| 19. Acetabular carina | 0 | 0 | 0 | 0 | 0 | 0 |
| 20. Omaulus | 1 | 1 | 1 | 1 | 1 | 1 |
| 21. Episternal sulcus | 0 | 0 | 0 | 0 | 0 | 0 |
| 22. Hypersternaulus | 1 | 1 | 1 | 1 | 1 | 1 |
| 23. Orientation of hypersternaulus | na | na | na | na | na | na |
| 24. Scrobal sulcus | 1 | 1 | 1 | 1 | 1 | 1 |
| 25. ♂ midbasitarsus | 1 | 1 | 1 | 0 | 0 | |
| 26. Hindtibial spines | 1 | 2 | 2 | 2 | 2 | 2 |
| 27. Propodeal enclosure | 1 | 1 | 1 | 1 | 1 | 1 |
| 28. Stigma size | 1 | 1 | 1 | 1 | 1 | 1 |
| 29. Stigma shape | 0 | 0 | 1 | 1 | 1 | 1 |
| 30. Stigma pore field | 0 | 0 | 0 | 0 | 0 | 0 |
| 31. Marginal cell size | 1 | 1 | 1 | 1 | 1 | 1 |
| 32. Marginal cell veins | 0 | 0 | 0 | 1 | 1 | 1 |
| 33. Submarginal cells | 1 | 1 | 1 | 1 | 1 | 0, 1, 2 |
| 34. Submarginal position | 0 | 1 | 0 | 0 | 0 | 0 |
| 35. Submarginal veins | 0 | 0 | 0 | 0 | 0 | 0, 1 |
| 36. Discoidal cell number | 1 | 1 | 1 | 1 | 1 | 1 |
| 37. Media divergence | 0 | 0 | 2 | 2 | 2 | na |
| 38. Submedian cell | 0 | 0 | 0 | 0 | 0 | na |
| 39. Hind wing cells | 0 | 0 | 0 | 0 | 0 | 1 |
| 40. Petiole length | 0 | 0 | 0 | 0 | 0 | 0 |
| 41. Petiolar sculpture | na | na | na | na | na | na |
| 42. Sternum I carinae | 0 | 0 | 0 | 0 | 0 | 0 |
| 43. S1 basal groove | 1 | 1 | 1 | 1 | 1 | 1 |
| 44. T1 lateral carina | 1 | 1 | 1 | 1 | 1 | 1 |
| 45. S2 microsetae | 0 | 0 | 0 | 0 | 0 | 0 |
| 46. Pygidial Plate | 0 | 0 | 0 | 0 | 2 | 2 |
| 47. Male Sternum 8 | 4 | 4 | 2 | 2 | 2 | 2 |
| 48. Genitalia | 0 | 0 | 1 | 1 | 1 | |
| 49. Microsculpture | 0 | 0 | 0 | 0 | 0 | 1 |

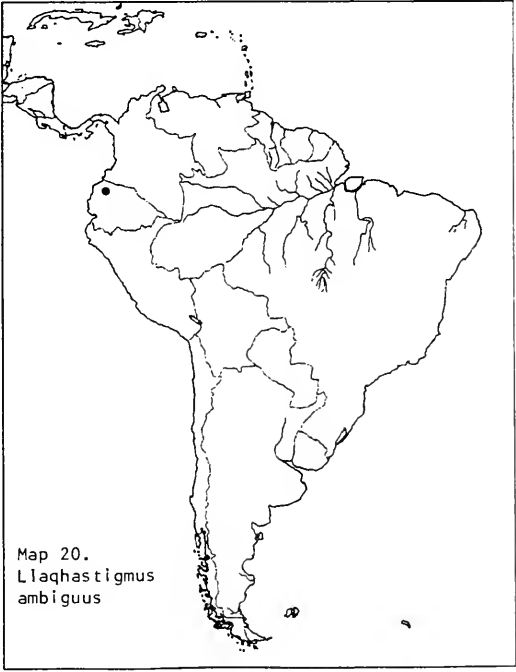
0 = plesiotypic character state, 1-6 = apotypic character states, na = not applicable, blank cells indicate specimens were unavailable and character state could not be determined from literature. Pulv = *Pulverro*, Ammops = *Ammoplanops*, Ammous = *Ammoplanus*, Paramo = *Parammoplanus*, Ammoplus = *Ammoplanellus*, Timber = *Timberlakeua*.

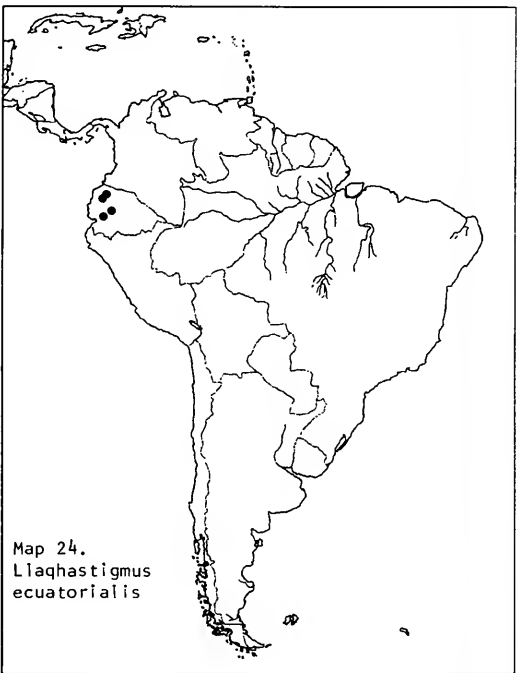
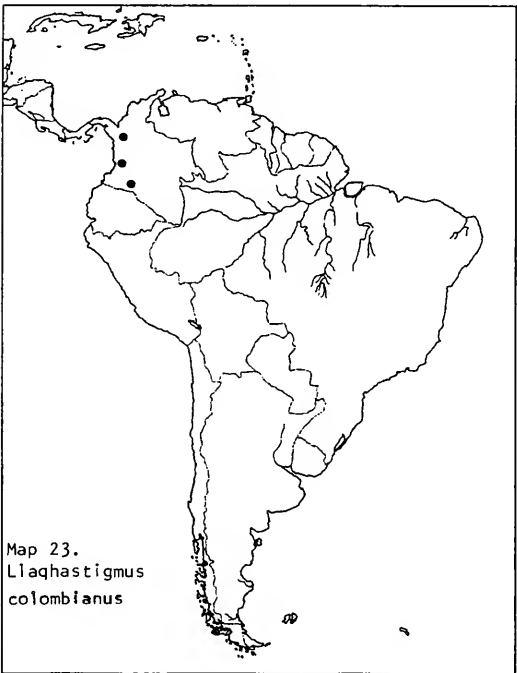
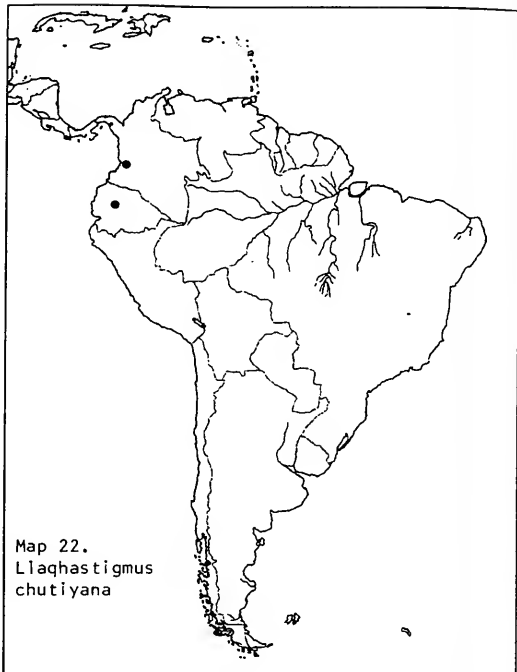


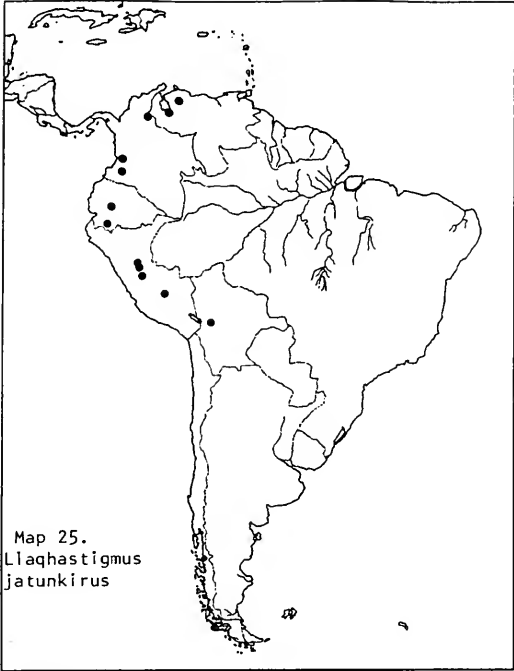


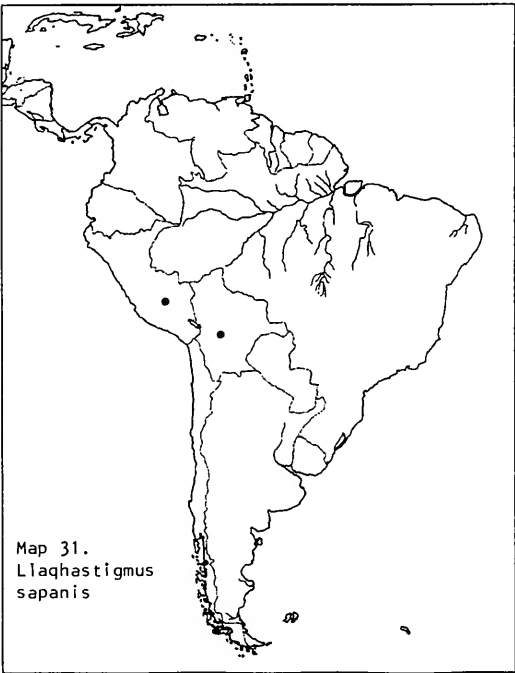
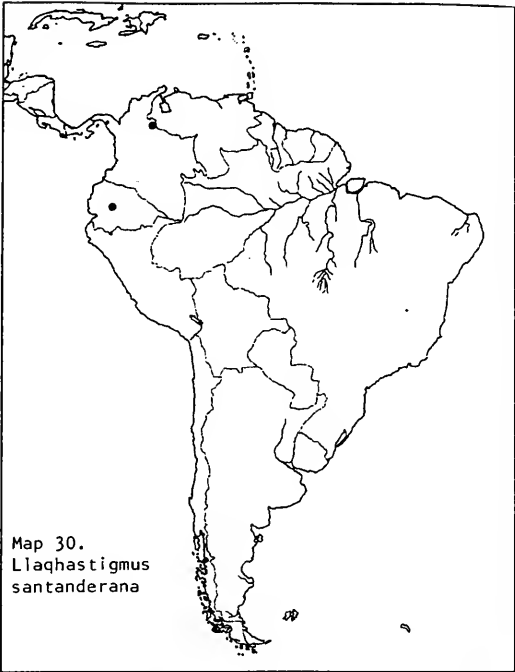
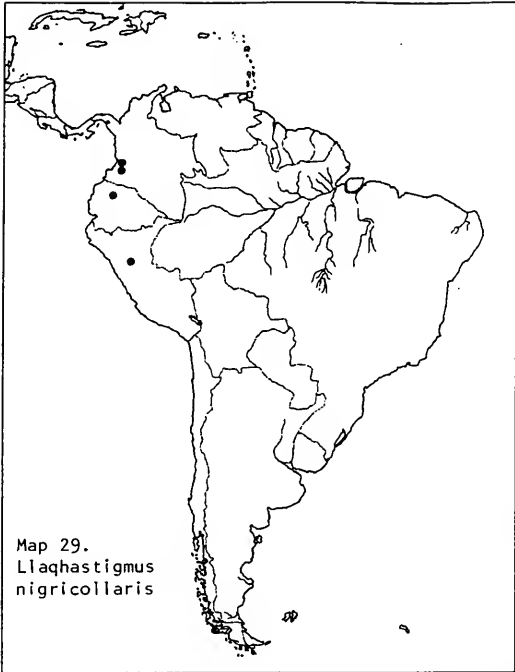


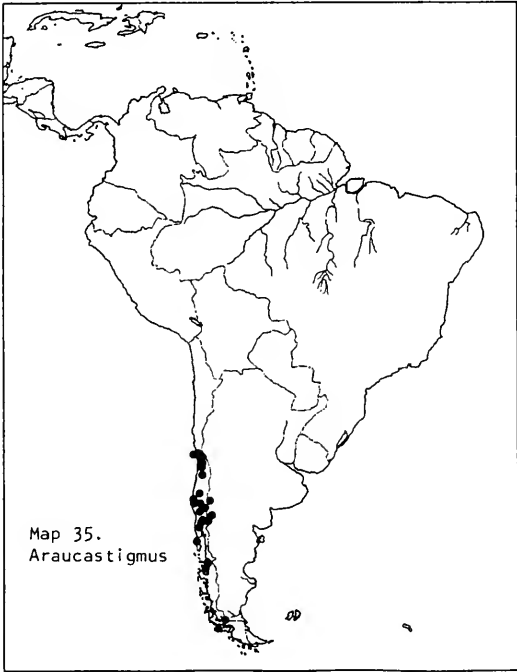
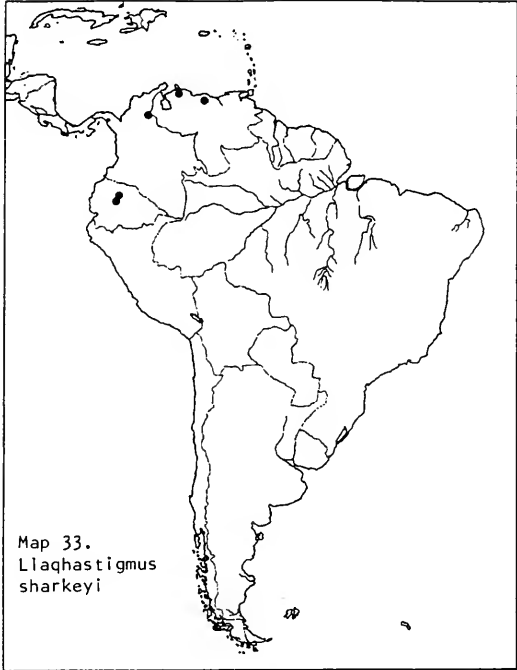


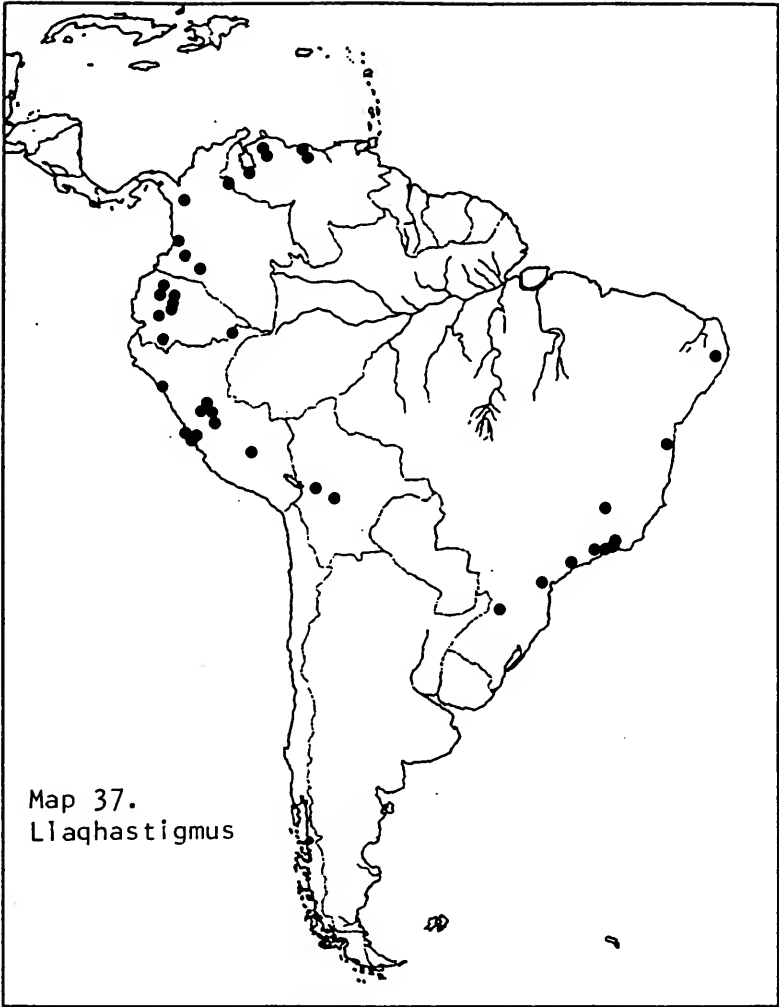












The Family-Group Names of the Ichneumoninae (Hymenoptera: Ichneumonidae)

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Abstract.—The family-group names in the subfamily Ichneumoninae are listed. Valid names are in accordance with the *International Code of Zoological Nomenclature* and differences with the names used by Townes are discussed. The historical background to Townes' rejection of certain Opinions of the International Commission for Zoological Nomenclature is examined; we conclude Townes was in error.

The subfamily Ichneumoninae constitutes an exceedingly large and diverse group of parasitoid wasps, and is one of the most taxonomically and nomenclaturally confusing groups of ichneumonids. The genera were never revised by Townes as part of his monographs of ichneumonid subfamilies. His taxonomic ideas on the subfamily were recorded in the regional catalogs put out by him and his collaborators (Townes *et al* 1961; Townes *et al* 1965; Townes & Townes 1966; Townes & Townes 1973). These groupings and generic concepts are often at odds with those of other authors, most notably Heinrich, who published monographs on the ichneumonines of the Nearctic, sub-Saharan Africa, and Southeast Asia. The situation is especially confusing because Townes based family-group names on the oldest included genus and refused to recognize the validity of certain Opinions issued by the International Commission for Zoological Nomenclature (hereafter referred to as "the Commission") (Townes 1969). While Heinrich endeavored to use nomenclature in accordance with the *International Code of Zoological Nomenclature* (International Commission for Zoological Nomencla-

ture 1985; hereafter referred to as "the Code"), he sometimes used junior synonyms of his own authorship in preference to older names of other authors or failed to cite proper dates and authorship for family-group names (cf. Protichneumonini Heinrich, 1934 vs. Heresiarchini Ashmead, 1900, and Ichneumonini Ashmead, 1895 instead of Ichneumonini Latreille, 1802 (Heinrich 1977: 10, 57).

TOWNES AND OPINION 159

Townes (1957, 1969) wrote at length about his reasons for considering certain Opinions of the Commission invalid. The following summarizes Townes' general views: "There is, however, a spurious "Opinion of the International Commission" (no. 178) that was published under the personal responsibility of Francis Hemming, without the knowledge or consent of the International Commission, and without an official vote of the Commission on the matter. Citations of this "Opinion" have been misleading. (Townes & Townes 1981). Most hymenopterists, outside of ichneumonid specialists, do not accept Townes' arguments (Day 1981 is an exception). Townes' extensive ichneumonid work has lead many

students of that group to follow his nomenclature. We do not, however, accept Townes' position or his supporting version of history; a detailed account of our view is given in Appendix I. Opinion 159, which deals with application of the ichneumonid names *Ichneumon*, *Pimpla*, and *Ephialtes*, is considered by us to be a valid publication of the Commission.

TRIBAL CONCEPTS

Correct nomenclature for family-group taxa in Ichneumonidae, excluding Ichneumoninae, has been published by Fitton & Gauld (1976; 1978). We here present the results of our investigations of ichneumonine family-group names, using the *Code* to determine the validity of the 46 names.

As mentioned above, Townes and Heinrich disagreed on the matter of tribal boundaries and composition (Gauld 1984: 184–185). In the absence of a worldwide monographic treatment of the subfamily, we have for the most part adopted the tribal classification used by Gauld (1984). Townes had intended to treat the subfamily as a fifth volume of his series of generic monographs but funding and health problems interfered. Townes' thoughts on ichneumonine classification are reflected in his regional catalogs and in the arrangement of the American Entomological Institute collection.

Before proceeding with a listing of the family-group names, we give a brief consideration of problems in certain tribes and subtribes.

1. **Alomyini-Phaeogenini-Heterischnini.** Confusion reigns concerning the composition of the tribe. European authors (Perkins 1959; Diller 1981; Rasnitsyn & Siitan 1981) have traditionally placed *Alomya* in a tribe or subfamily of its own. Townes consistently put it with the group of genera, centered about *Phaeogenes*, that previously cited workers referred to as Phaeogenini. Townes believed *Alomya* to be closely related to *Cen-*

teterus and *Colpognathus*, genera placed by others in Phaeogenini (Townes, pers. comm. to DBW). Moreover, Townes placed the genera *Heterischnus* and *Lusius* in a separate tribe, Heterischnini. Perkins, Diller, and Rasnitsyn & Siitan have all maintained *Heterischnus* in the Phaeogenini. Wahl is examining the relationships of these genera as part of a forthcoming revision; preliminary results indicate that all the aforementioned genera constitute a monophyletic group, and they are here treated as one tribe. With the inclusion of *Alomya*, the correct tribal name is Alomyini; Townes & Townes (1951: 276) having made a first-revisor decision between the Förster names Alomyoidae and Phaeogenoidae (published simultaneously in 1869). The subtribal divisions of Diller (1981; 1994) are not used here, pending further study.

2. **Platylabini-Eurylabini-Zimmeriini.** Townes (Townes *et al* 1961; Townes *et al* 1965; Townes & Townes 1973) consistently placed the genera *Eurylabus* and *Cotihersiarches* (= *Zimmeria*) in the Platylabini. Other authors (Heinrich 1967, 1974; Perkins 1959; Rasnitsyn & Siitan 1981) put them in the Eurylabini and Zimmeriini, respectively. When Heinrich (1934) first described the Eurylabini, he recognized the *Eurylabus* group and the *Goedartia* group. Townes (Townes *et al* 1961) broke up the tribe, placing *Eurylabus* in the Platylabini and the *Goedartia* group in its own tribe, Goedartiini. Neither *Eurylabus* nor *Cotihersiarches* exhibits the characteristic small convex clypeus of *Platylabus* and its relatives, and only *Cotihersiarches* has a flattened petiole. Until detailed studies are made on platylabine generic relationships, we believe it best for now to recognize Eurylabini and Zimmeriini as separate tribes.

3. **Goedartiini-Compophorini.** When originally proposed by Townes *et al* (1961), Goedartiini included *Goedartia*, *Maraces*, *Charitojoppa*, and *Habrojoppa*. Compophorini was described by Hein-

rich (1967) and included *Compsophorus*, *Oxyjoppa*, *Eccoptosagellus*, *Tosquinetia*, *Epjoppa*, *Charitojoppa*, *Habrojoppa*, and *Pyramidamblys*; *Goedartia* was explicitly excluded from the tribe. Townes (Townes & Townes 1973) synonymized Heinrich's Compsophorini under Goedartiini. Heinrich (1975) placed only *Goedartia*, *Maraces*, and *Pseudomaraces* in Goedartiini, retaining his original concept of two tribes.

Townes' concept of Goedartiini is based on: 1) a wide mandible that is not tapered apically, 2) the occipital carina that meets the hypostomal carina at the mandibular base, and 3) the cell 1+2Rs (areolet) of the fore wing that is pointed above, not truncate (Townes *et al* 1961). Heinrich (1967) pointed out that *Goedartia* differs from *Compsophorus* and its relatives in many details of the head and mesosoma, including the male flagellum. Until fundamental studies are made of the relationships within the stenopneusticine Ichneumoninae, it seems best to maintain Heinrich's concept of two tribes.

4. **Ichneumonini.** As mentioned previously, we accept that Opinion 159 of the Commission was validly issued. Accordingly, Ichneumonini is the correct name for the tribe that Townes called Joppini. Gyrodontini was used by Carlson (1979) due to Heinrich's belief that Joppini was strictly a Neotropical group (G. Heinrich, pers. comm. to R.W. Carlson). If one believes the Townes position to be correct, it should be noted that Joppini is the correct tribal name. The Joppini of Townes and Ichneumonini of Heinrich are essentially the same except that Heinrich placed *Pseudoplatylabus*, *Acanthojoppa*, and related genera in the Joppocryptini (referred to as Acanthojoppini in Heinrich's publications) and placed *Tetragonochora* in a tribe of its own (Heinrich, 1934).

5. **Amblytelina.** Amblytelina based on *Amblyteles* Wesmael is a junior homonym of Amblytelides Blackburn, 1892 (Blackburn, 1892) based on the coleopterous genus *Amblytelus* Erichson (Carabidae). Carl-

son (1979) emended Amblytelina to Amblytelesina but this is not in accordance with the *Code*, as such cases are to be referred to the Commission. A request to the Commission is being prepared.

6. **Protichneumonini-Heresiarchini.** Townes called this tribe Ichneumonini, due to his views on the validity of Opinion 159. Carlson (1979) and Gupta (1987) have used this interpretation as well, but all other authors have used Protichneumonini. Depending upon the treatment of *Heresiarches* and related genera, however, Protichneumonini may not be the correct name. Perkins (1959) and Rasnitsyn & Sittan (1981) maintain *Heresiarches* in a separate tribe, Heresiarchini. Townes always kept the genus in his Ichneumonini and Heinrich did likewise in the equivalent Protichneumonini. Heinrich (Heinrich 1960: 21) discussed the situation and he later recognized the group as a subtribe of Protichneumonini. This arrangement necessitates changing the tribal name to Heresiarchini, as pointed out by Perkins (1959: 28fn).

7. **Trogini.** Trogini based on *Trogus* Panzer is a junior homonym of Trogidae MacLeay, 1819 (MacLeay, 1819), based on the coleopterous genus *Trox* Fabricius (Trogidae). Carlson (1979) emended Trogini to Trogusini but this is not in accordance with the *Code*, as such cases are to be referred to the Commission. A request to the Commission is being prepared.

Heinrich placed *Callajoppa* and related genera in the Trogini as a subtribe, Callajoppina. Townes instead put these genera in the Heresiarchini, restricting Trogini to the parasitoids of Papilionidae and other Papilionoidea. This arrangement is followed here but it should be noted that the *Callajoppa*-group is part of a continuum linking certain Heresiarchini with the Trogini (Gauld 1984: 184-185; Heinrich 1968: 82, 1977: 284), thus making the placement of this group in one tribe or another a subjective decision.

FAMILY-GROUP NAMES OF THE
ICHNEUMONINAE
ICHNEUMONINAE Latreille, 1802.

1. **Alomyini** Förster, 1869 (incl. Heterischnini of Townes)
Alomyoidae Förster, 1869: 144, 194. Type-genus: *Alomya* Panzer.
Phaeogenoidae Förster, 1869: 144, 191. Type-genus: *Phaeogenes* Wesmael.
Dicaelotina Holmgren, 1889: 343. Type-genus: *Dicaelotus* Wesmael.
Diadromina Holmgren, 1889: 345. Type-genus: *Diadromus* Wesmael.
Epitomina Holmgren, 1889: 347. Type-genus: *Epitomus* Förster.
Gnathoxina Holmgren, 1889: 344. Type-genus: *Gnathoxys* Wesmael.
Herpestomina Holmgren, 1889: 344. Type-genus: *Herpestomus* Wesmael.
Oronotina Holmgren, 1889: 343. Type-genus: *Oronotus* Wesmael.
Stenodotina Schmiedeknecht, 1903: 262. Type-genus: *Stenodontus* Berthoumieu.
Heterischnini Townes *et al*, 1961: 337, 458. Type-genus: *Heterischnus* Wesmael.
Chauviniina Diller, 1981: 95, 98. Type-genus: *Chauvinia* Heinrich.
Dicaelodontina Diller, 1994: 126. Type-genus: *Dicaelodontus* Diller.
2. **Platylabini** Berthoumieu, 1904. (= Pristicerotini of Townes)
Platylabini Berthoumieu, 1904: 4. Type-genus: *Platylabus* Wesmael.
[Pristiceratini Townes & Townes, 1951: 280. Not available under Article 13 of the Code. Incorrect spelling.]
Pristicerotini Townes *et al*, 1961: 393, 458. Type-genus: *Pristicerus* Gravenhorst.
3. **Eurylabini** Heinrich, 1934.
Eurylabini Heinrich, 1934: 64-67. Type-genus: *Eurylabus* Wesmael.
4. **Zimmeriini** Heinrich, 1934.
[Zimmerini Heinrich, 1934: 67. Type-genus: (*Zimmeria* Heinrich) = *Cotiheresiarches* Telenga. Incorrectly formed stem.]
Zimmeriini Heinrich; Rasnitsyn & Siitan, 1981: 510. Justified emendation.
5. **Ceratojoppini** Heinrich, 1938.
Ceratojoppini Heinrich, 1938: 25, 121. Type-genus: *Ceratojoppa* Cameron.
6. **Ctenocalini** Heinrich, 1938.
Ctenocalini Heinrich, 1938: 25, 40-41. Type-genus: *Ctenocalus* Szepligeti.
7. **Goedartiini** Townes *et al*, 1961.
Goedartiini Townes *et al*, 1961: 399, 458. Type-genus: *Goedartia* Boie.
8. **Compsophorini** Heinrich, 1967.
[Compsophorina Heinrich, 1962: 688. Not available under Article 13 of the Code.]
Compsophorini Heinrich, 1967: 25. Type-genus: *Compsophorus* Saussure.
9. **Ischnojoppini** Heinrich, 1938.
Ischnojoppini Heinrich, 1938: 25, 117. Type-genus: *Ischnojoppa* Kriechbaumer.
10. **Listrodromini** Förster, 1869.
Listrodromoidae Förster, 1869: 144, 194. Type-genus: *Listrodromus* Wesmael.
11. **Oedicephalini** Heinrich, 1934. (= Notosemi of Townes)
Oedicephalini Heinrich, 1934: 67, 118-119. Type-genus: *Oedicephalus* Cresson.
Notosemi Townes *et al*, 1961: 338, 459. Type-genus: *Notosemus* Förster.
12. **Ichneumonini** Latreille, 1802. (= Joppini of Townes in part)
(The following are *incertae sedis* within the tribe, as the type genera were never formally assigned to a subtribe by Heinrich:
Joppinen Kriechbaumer, 1898: 2. Type-genus: *Joppa* Fabricius.
Merolidini Brèthes, 1909. Type-genus: *Merolides* Brèthes. (The type and sole specimen of *Merolides arechavaletai* Brèthes is lost; Townes (1966; pers. comm.) placed it in Joppini, near *Limerodes*.)
Tetragonochorini Heinrich, 1934: 64, 67. Type-genus: *Tetragonochora* Kriechbaumer. (Townes (Townes & Townes, 1966) placed this genus in his Joppini.)
- a. **Ichneumonina** Latreille, 1802.
Ichneumonides Latreille, 1802: 318. Type-genus: *Ichneumon* Linnaeus.
[Pterocorminae Heinrich, 1949: 256. Not available under Article 13 of the Code.]
- b. **Gyrodontina** Schmiedeknecht, 1902.
Gyrodontini Schmiedeknecht, 1902: 9, 28. Type-genus: *Gyrodonta* Cameron.

- Cratichneumonina Heinrich, 1967: 27. Type-genus: *Cratichneumon* Thomson.
- [c. **Amblytelina** Viereck, 1918.]
[Amblytelinae Viereck, 1918: 74. Type-genus: *Amblyteles* Wesmael. Amblytelina based on *Amblyteles* Wesmael is a junior homonym of Amblytelides Blackburn, 1892 (Blackburn, 1892: 85), based on the coleopterous genus *Amblytelus* Erichson (Carabidae)]
[Amblytelesina Carlson, 1979: 507. Illegal emendation. Article 55(b) of the *Code*.]
- d. **Hoplismenina** Heinrich, 1967.
Hoplismenina Heinrich, 1967: 26. Type-genus: *Hoplismenus* Gravenhorst.
- e. **Aethioplitina** Heinrich, 1967.
Aethioplitina Heinrich, 1967: 27. Type-genus: *Aethioplites* Heinrich.
13. **Joppocryptini** Viereck, 1918.
Joppocryptinae Viereck, 1918: 73. Type-genus: *Joppocryptus* Viereck.
Acanthojoppini Heinrich, 1934: 65, 67, 138. Type-genus: (*Acanthojoppa* Cameron) = *Eccoptosage* Kriechbaumer. Townes (1966) placed this genus in his Joppini.
14. **Heresiarchini** Ashmead, 1900 (= Ichneumonini of Townes; includes part of Trogini of Heinrich).
- a. **Protichneumonina** Heinrich, 1934.
Protichneumonini Heinrich, 1934: 66, 84. Type-genus: *Protichneumon* Thomson.
- b. **Heresiarchina** Ashmead, 1900.
Heresiarchini Ashmead, 1900: 567. Type-genus: *Heresiarches* Wesmael.
- c. **Apatetorina** Heinrich, 1967.
Apatetorina Heinrich, 1967: 26, 50. Type-genus: *Apatetor* Saussure.
- d. **Callajoppina** Heinrich, 1962.
Callajoppina Heinrich, 1962: 809–810. Type-genus: *Callajoppa* Cameron.
- [15. **Trogini** Förster, 1869.]
[Trogidae Förster, 1869: 144, 188. Type-genus: *Trogus* Panzer. Trogini based on *Trogus* Panzer is a junior homonym of Trogidae MacLeay, 1819 (MacLeay, 1819: 136), based on the coleopterous genus *Trox* Fabricius. Although Förster cites *Trogus* Gravenhorst, Gravenhorst includ-

ed the type species of *Trogus* Panzer in his treatment of the genus and had the same generic concept]
[Trogusina Carlson, 1979: 538. Illegal emendation. Article 55(b) of the *Code*.]

ACKNOWLEDGEMENTS

Robert Carlson's generosity in sharing his list of ichneumonid family-group names is gratefully acknowledged. We wish to thank the following for their advice and comments: John Barron, Yves Bosquet, Terry Erwin, Ian Gauld, Henri Goulet, C.D. Michener, Charles Porter, Alexandr Rasnitsyn, Michael Sharkey, G. Stuart Walley, and Robert Wharton.

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APPENDIX 1

Townes' arguments regarding the invalidity of Opinion 159 were put forth in Townes (1957, 1969); his version of the relevant events may be summarized as follows from these two references except where otherwise noted:

1913—At the Monaco International Congress of Zoology, the Commission was delegated authority to suspend the Rules and declare on various cases, on the authority of the Congress. Suspensions could be made only under the following procedures:

- Not less than one year's notice that such a suspension is under consideration in two or more of five specified publications.
- The votes of the Commission is unanimous in favor of suspension.
- If the vote is a $\frac{2}{3}$ majority of the full Commission, but not unanimous, in favor of suspension, the Commission must report the facts to the next Congress (where specified arbitration would be made.)

1935—J.C. Bradley presented a list of generic names at the Commission meeting in Lisbon, requesting suspension of the Rules in these cases. Bradley requested new type-species designations for *Ichneumon*, *Pimpla*, and *Ephialtes*. Six out of 18 Commissioners attended the Lisbon meeting and six temporary Commissioners were appointed. Ten out of 12 were present when the Bradley proposal was presented and approved. No notice of intention to consider these names had been published in advance of the Lisbon meeting.

1936—When it was pointed out that the required advance notice had not been published regarding the proposed changes, the Commission published notices in 1936 that it would officially consider Bradley's list at some future time.

1939—Karl Jordan and Francis Hemming met and made a decision between themselves. The authority for their action was that upon adjournment of the Lisbon sessions, they were to "take such other action as might appear to them necessary or expedient . . . to give effect to the decisions reached by the Commission at the Lisbon Session . . ." (Hemming 1945a). "The direction upon adjournment of the Lisbon meeting of the Commissioners to Jordan and Hemming to put into effect the decisions of the meeting did not give Jordan and Hemming power to make the decisions . . ." (Townes 1957).

1943—Following this, Bradley's proposals never came up again for decision. Townes contacted James L. Peters, the acting secretary at Lisbon and asked whether any further action had been taken on the Bradley names. Peters replied that the question of the ichneumonid names had never been circulated. Furthermore, he stated that "no vote had been taken on the subject of these three names . . ." (Townes 1969).

Townes thus concluded that the Commission never took action. According to Townes, Hemming argued the requirements for suspending the Rules had been met by: 1) a vote in 1935 before publication of the cases, 2) publication in 1936 that the cases would be considered, 3) the fact that no Commissioner wrote him after 1936 with objections. Townes rejects these arguments because: 1) the vote must be taken after publication, 2) only 12 Commissioners were in Lisbon and only ten in the actual meeting, while the requirement is for a unanimous vote by all 18 Commissioners, 3) awaiting unsolicited letters is not the same as an actual request for a vote. Finally, Townes noted that the Bradley petition, signed by 59 hymenopterists, was circulated in 1928 and is not the same as that presented in 1935, except in the case of *Cryptus*. The type-species for *Ichneumon*, *Ephialtes*, and *Pimpla* are the same recognized by Townes.

This recounting, however, omits crucial information. While the Monaco Congress listed the conditions under which the Rules could ordinarily be suspended, Secretary C.W. Stiles (*Compte Rendu* 1913: 892-893) pointed out the following: "Upon a unanimous vote, 'By-Laws' may be temporarily 'suspended', that is to say, they may be set aside and the body takes action on the matter under consideration unrestricted by the provisions of the By-Laws; and such action, if taken under a 'Special Rule' framed for the case at hand or without reference to any rules, except the 'Constitution' and recognized 'Parliamentary Rules', has all the validity

of an action taken under the "By-Laws". Thus, if the Congress confers upon the Commission the plenary power to suspend the Règles in any given case, it practically says to the Commission: "If you carry out the precautions provided for in the Supplemental Report, you may decide any given case arbitrarily without reference to the Règles or you may make a "Special Rule" to govern that particular case, and this Congress will accept your decision as being just as authoritative as if you had made this ruling strictly in accord with the Code." A plan of this kind is thoroughly in accord with recognized parliamentary customs and it has the great advantage of avoiding the necessity of introducing "Exceptions" to the Rules." This is the background against which the events of 1935 occurred.

Contrary to Townes' statement, Bradley's petition of 1935 was the same as that circulated in 1928. It was presented to the International Committee of Entomological Nomenclature (ICEN) in Madrid in the week preceding the opening of the Twelfth International Congress of Zoology in Lisbon (Hemming 1943a). The petition was considered and a number of proposals were made by the ICEN concerning resolution of the problems (Hemming 1945a: 282).

The ICEN's recommendations for this and other cases were laid before the Commission at its second meeting on 16 Sept. 1935. Because it had not been possible for the Commission to meet prior to the Congress, there were only 2½ days to discuss the cases and prepare a report to the Congress. President Jordan felt it best to take the pending cases into immediate consideration and "for this purpose suspend the By-laws of the Commission to such extent as might be necessary for the period of the present Congress." (Hemming 1943b: 10-11). At that meeting, 10 out of 11 Commissioners present in Lisbon were in attendance; Walter Arndt, an alternate, did not attend the five Commission meetings and Teiso Esaki was elected to the Commission at this particular session. The attending Commissioners passed the usual parliamentary unanimous consent to suspend the By-laws (note this was not an *emendation* of the By-Laws, which would have required an affirmative vote of 12 members (ICZN By-laws, Article VIII, Sect. 1)). It was agreed to give immediate consideration to all submitted cases that it was felt had reached the stage at which a decision could be made. To give effect to this, use would be made of the By-law suspension that had just been agreed upon. Since this involved violating the normal procedures for "suspension of the Règles" in that the prescribed advertisement had not been published one year previously, the various cases and the Commission's decisions would be advertised as soon as possible after the conclusion of the Lisbon meetings and no Opinions would be published until after one year from the date of the advertisement's dispatch. Nowhere does Townes, in his recounting,

mention that the Commission suspended its By-laws, as provided by parliamentary procedures.

At the Commission's third session, it agreed "under suspension of the Rules" to set aside current type designations for the names on the Bradley list and declare new ones. For ichneumonids, the Commission agreed to reject *Ephialtes* Schrank 1802 and to designate the following type species:

Ichneumon L.: *Ichneumon extensorius* L.

Pimpla Fabricius: *Ichneumon instigator* Fabricius

Ephialtes Gravenhorst: *Ichneumon manifestor* L.

The Commission "came to the conclusion that the more radical of the proposals submitted by the [ICEN] provided the most satisfactory solution of the difficulties presented by the present case." (Hemming 1945a: 282). Townes neglected to mention the ICEN involvement and chose to portray the Commission decisions as part of an illegal and arbitrary process.

The Commission's fifth meeting on 18 Sept. 1935 saw 11 of the 12 Commissioners present; it was agreed that President Jordan "and the new Secretary, when elected, should be authorized to make such arrangements, and to take such actions, as might appear to them necessary or expedient . . ." and "to secure the due publication of the Opinions agreed upon from time to time by the Commission at their Lisbon Session." (Hemming 1943b: 48). The Commission also unanimously agreed to adopt as their report to the Congress the draft prepared by Hemming (*ibid.*, p. 47). This report (Hemming 1943c), which duly noted the suspension of the By-laws, was approved by the Congress (Anonymous, 1943).

Notice of the possible suspension of the Rules was published in May 1936 (Stiles 1936). Except for Townes' allegation, there is no evidence that the advertisement was published at the urging of scientists concerned that no published notices had been made prior to the Lisbon sessions. It was done on the authority of the Commission operating under the suspension of the By-laws.

After the 1936 advertisement, one communication was received regarding the ichneumonid names. It bore the signature of S.A. Rohwer in the name of the Committee on Nomenclature of the Entomological Society of Washington (Hemming 1945a). The letter was against the proposed new type-species; appended to the letter was a note of dissent, in favor of the proposed *nomina conservanda*, by R.A. Cushman, one of the prominent ichneumonologists of the day.

Copies of the letter were immediately sent to the other Commissioners but no member expressed himself as agreeing with the Rohwer point of view (*ibid.*, p. 286). Jordan and Hemming met on 19 June 1939 under the authority of the Resolution adopted by the Commission on 18 Sept. 1935 (Hemming 1945b). They took note that no Commissioner had responded to the Rohwer communication. In their opinion, no new facts had been brought forth that were not before

the Commission in 1935. Given this, they “decided the proper course . . . was to give effect to the decisions in this matter reached by the International Commission at the Lisbon Session . . . and therefore that Opinions should be issued as soon as possible.” (Hemming 1945a: 287). The resulting Opinion 159 was published in 1945 (ibid.).

Townes was preparing to publish a catalog of Nearctic Ichneumonidae (Townes 1944-1945) when he wrote to Peters in 1943. He took Peters’ advice and used names based on priority; they both apparently expected the matter to be voted on by the Commission, with the outcome uncertain. Jordan and Hemming, however, were given the authority to make decisions by virtue of the Commission acting under the valid suspension of the By-laws. Townes’ objections to Hemming’s listing of the usual procedures for suspending the Rules (i.e., one year’s notice of suspension in two or more of five journals, etc) are irrelevant. Hemming apparently used these stock phrases as boilerplate.

At this point, the reader might wonder why such effort has been spent on an arcane issue. From our viewpoints as ichneumonologists, it is important that Townes’ arguments be put to rest in order to attain a stable ichneumonid nomenclature. Outside Ichneumonidae, there always remains the possibility that someone will read Townes’ version of events and raise havoc in groups that heretofore have attained relative nomenclatural stability.

In summary, rejection of Townes’ arguments gives the following generic names:

Pimplinae

Ephialtini (= Pimplini of Townes)

| ICZN name | Townes name |
|--|--|
| <i>Ephialtes</i> Gravenhorst, 1829 | <i>Pimpla</i> Fabricius, 1804 |
| (type-species: <i>Ichneumon manifestor</i> L.) | (type-species: <i>Ichneumon manifestor</i> L.) |

Pimplini (= Ephialtini of Townes)

| ICZN name | Townes name |
|--|---|
| <i>Apechthis</i> Förster, 1869 | <i>Ephialtes</i> Schrank, 1802 |
| (type-species: <i>Ichneumon rufatus</i> L.) | (type-species: <i>Ichneumon compunctor</i> L.) |
| <i>Pimpla</i> Fabricius, 1804 | <i>Coccygomimus</i> Saussure, 1892 |
| (type-species: <i>Ichneumon instigator</i> L.) | (type-species: <i>Coccygomimus madecassus</i> Saussure) |

Ichneumoninae

Ichneumonini (= Joppini of Townes)

| ICZN name | Townes name |
|---|---|
| <i>Ichneumon</i> L., 1758 | <i>Pterocormus</i> Förster, 1850 |
| (type-species: <i>Ichneumon extensorius</i> L.) | (type-species: <i>Ichneumon latrator</i> Fabricius) |

Heresiarchini (= Ichneumonini of Townes, Proti-
chneumonini of Heinrich)

| ICZN name | Townes name |
|---|---|
| <i>Coelichneumon</i> Thomson, 1893 | <i>Ichneumon</i> L., 1758 |
| (type-species: <i>Ichneumon comitator</i> L.) | (type-species: <i>Ichneumon comitator</i> L.) |

CONSTITUTION AND BYLAWS OF THE INTERNATIONAL SOCIETY OF HYMENOPTERISTS

CONSTITUTION

ARTICLE I

- Section 1. This organization shall be known as the International Society of Hymenopterists.
- Section 2. The objectives of the Society shall be to encourage scientific research and to promote the diffusion of scientific knowledge concerning Hymenoptera.

ARTICLE II

- Section 1. The membership of the Society shall consist of Active Members, Student Members, Emeritus Members, and Sustaining Members.
- Section 2. Active Members shall be individuals who are interested in Hymenoptera and the objectives of the Society. Each Active Member shall pay to the Society annual dues as prescribed in the Bylaws.
- Section 3. Student Members shall be full-time undergraduate, or part-time or full-time graduate students at a recognized institution of higher learning. Each Student Member shall pay to the Society annual dues as prescribed in the Bylaws. To qualify for Student Membership, a student must have his or her status verified by a faculty member at his or her institution. Student Members shall have all the rights and privileges of active membership except holding office.
- Section 4. Emeritus Members shall be members who have retired from active service, and who petition the Executive Committee for a change in classification. Election to Emeritus Membership requires a three-fourths vote of the Executive Committee present or voting by mail. Emeritus Members shall have all rights and privileges of active membership except holding office, and shall be released from payment of dues. Emeritus Members may subscribe to any journals published by the Society with the payment of subscription fees.
- Section 5. Sustaining Members shall be educational or commercial institutions, or individuals interested in the promotion and advancement of the study of Hymenoptera, and who are in sympathy with the objectives of the Society. Annual dues shall be paid as prescribed in the Bylaws.

ARTICLE III

- Section 1. The officers of the Society shall consist of a President, a President-Elect, an Editor (when and if the Society publishes a journal), a Secretary, and a Treasurer. The President-Elect shall serve for two years, and then automatically assume the office of President for two years. The Editor, Secretary, and Treasurer shall each serve for four years.
- Section 2. The elected officers shall take office at the close of the business session of the next scheduled meeting of the Society following their election and shall hold office until their successors have been elected and take office.

ARTICLE IV

- Section 1. The President shall discharge the usual duties of a presiding officer at the meetings of the Society and the Executive Committee.

- Section 2. The President-Elect shall assume the duties of the President in the event of his or her absence. In the event that both the President and President-Elect are absent at a meeting, The President may appoint another member of the Executive Committee to serve as presiding officer.
- Section 3. The Editor shall assume editorial responsibility for any journals published by the Society. He or she shall be responsible for selecting and delegating the duties of any subject editors.
- Section 4. The Secretary shall keep the records of the Society. He or she shall be responsible for notifying the membership of meetings, calls for papers, dues, nominations, annual reports, and all other items as directed by the Executive Committee. He or she shall record minutes of meetings of the Society and Executive Committee, and maintain the record of names and address of members.
- Section 5. The Treasurer shall have custody of all funds of the Society and shall make routine disbursements as required. Unusual disbursements and/or investments shall be made only with the concurrence of the Executive Committee. He or she shall keep an account of receipts and disbursements and those accounts shall be audited as provided by the Executive Committee. He or she shall present a statement of the receipts and expenditures and funds for the past year at the business session of regular meetings of the Society.

ARTICLE V

- Section 1. The Executive Committee shall consist of the President, President-Elect, Editor (if elected), Secretary, and Treasurer.
- Section 2. The Executive Committee shall execute and administer the affairs of the Society during the interval between the regular meetings. It shall be responsible for authorizing all unusual expenditures by the Treasurer and shall fill temporary vacancies among the officers.

ARTICLE VI

- Section 1. The Executive Committee shall appoint a Nominating Committee of at least three members to serve for one year. The Nominating Committee shall solicit nominations for those vacancies on the Executive Committee that will occur in the following year. The Nominating Committee shall nominate at least two persons for each office and ascertain whether the proposed nominees will accept office if elected. The slate of nominees will be made available to the membership by the Secretary, and a mail ballot will be taken. The candidate who receives the majority of votes cast shall be declared elected.
- Section 2. The Executive Committee shall have the authority to appoint a member of the Society to fill the remainder of the term of any officer of the Society who is unable to continue for whatever reason.
- Section 3. Standing committees and ad hoc committees shall be appointed by the Executive Committee.

ARTICLE VII

- Section 1. The Society shall hold regular meetings as provided in the Bylaws. The Executive Committee may arrange for special meetings and/or joint programs with related scientific groups, and for presentation of papers.

ARTICLE VIII

- Section 1. Amendments to the Constitution of the Society may be proposed in writing by any member to the Executive Committee. Such proposed amendments as are approved by a majority vote of the Executive Committee shall be submitted to the members by mail ballot, and will be adopted by a favorable vote of two-thirds of the members voting.

ARTICLE IX

- Section 1. In the event of dissolution or termination of the International Society of Hymenopterists, title to and possession of all property of the Society shall pass forthwith to such organization, dedicated to similar purposes and qualified for exemption under Section 501(c)(3) of the Internal Revenue Code of 1954 (or corresponding provision of an future United States Internal Revenue Law), as the Executive Committee shall deem best qualified to carry on the functions of the Society.

BYLAWS

1. Annual dues for Active Members shall be \$25.00 US per year. Student Members shall pay \$15.00 US per year. Sustaining Members shall pay \$50.00 US per year. Dues may be waived upon request at the discretion of the Treasurer.
2. These Bylaws may be amended or suspended by a two-thirds vote of the members present at any regular meeting. New Bylaws may be adopted by a two-thirds vote of the members present at any regular meeting.
3. Regular annual meetings shall be held in conjunction with the annual meetings of the Entomological Society of America. Regular quadrennial international meetings shall be held as scheduled when and where by the Executive Committee.
4. Newly elected members of the Executive Committee shall take office at the regular meeting held in conjunction with the annual meeting of the Entomological Society of America following their election.

INSTRUCTIONS FOR AUTHORS

General Policy

The *Journal of Hymenoptera Research* invites papers of high scientific quality reporting comprehensive research on all aspects of Hymenoptera, including biology, behavior, ecology, systematics, taxonomy, genetics, and morphology. Taxonomic papers describing single species are unlikely to be accepted unless a strong case is evident, such as importance in economic entomology or with concurrent biology or ecology. Manuscript length generally should not exceed 50 typed pages; however, no upper limit on length has been set for papers of exceptional quality and importance, including taxonomic monographs at generic or higher level.

All papers will be reviewed by at least two referees. The referees will be chosen by the appropriate subject editor. However, it would be helpful if authors would submit the names of two persons who are competent to review the manuscript.

The language of publication is English. Summaries in other languages are acceptable.

The deadline for receipt of manuscripts is 1 February of each year.

Format and Preparation

Three copies of each manuscript, including copies of illustrations, should be submitted on letter size or A4 paper, double spaced, with at least 25 mm margins on all sides. On the upper left of the title page give name, address and telephone and fax numbers of the author to whom all correspondence is to be sent.

The paper should have a concise and informative title, followed by the names and addresses of all authors. The sequence of material should be: title, author(s), abstract, text, acknowledgments, literature cited, appendix, figure legends, figure copies (each numbered and identified), tables (each numbered and with heading). Each of the following should start a new page: (1) title page, (2) abstract, (3) text, (4) literature cited, (5) figure legends, (6) footnotes.

Following acceptance of the manuscript, the author should provide the editor with one copy of the manuscript accompanied by a copy on diskette using DD, double sided computer diskettes - IBM compatible MS DOS 5.25 inch or IBM and Macintosh 3.5 inch diskettes. (Authors who do not have access to a computer should submit three copies of the manuscript.) The paper may be submitted in most PC and Mac word processor programs such as Microsoft Word, FullWrite Professional, WordPerfect, WriteNow, Nisus, MacWrite, or MacWrite II. If possible, all words that must be italicized should be done so, not underscored. Use of the words male and female is preferred to sex symbols. Tables may be formatted in a spread sheet program such as MS Works or MS Excel. Text should be double spaced typing, with 25 mm left and right margins. Tables should be put in a separate file. Diskettes should be accompanied by the name of the software program used (e.g., WordPerfect, Microsoft Word). Authors should keep backup copies of all material sent to the Editor. The Society cannot be responsible for diskettes or text mislaid or destroyed in transit or during editing.

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All papers must conform to the *International Code of Zoological Nomenclature*. The first mention of a plant or animal should include the full scientific name including the authority. Genus names should not be abbreviated at the beginning of a sentence. In taxonomic papers type specimens must be clearly designated, type depositories must be clearly indicated, and new taxa must be clearly differentiated from existing taxa by means of keys or differential diagnoses. Authors are required to deposit all type material in internationally recognized institutions (not private collections). Voucher specimens should be designated for specimens used in behavioral or autecological studies, and they should be deposited similarly.

Acceptance of taxonomic papers will not require use of cladistic methods; however, authors using them will be expected to specify the phylogenetic program used (if any), including discussion of program options used. A data matrix should be provided if the subject is complex. Cladograms must be hung with characters and these should include descriptors (not numbers alone) when feasible. The number of parsimonious cladograms generated should be stated and the reasons for the one adopted. Lengths and consistency indices should be provided. Adequate discussions should be given for characters, plesiomorphic conditions, and distributions of characters among outgroups when problematical.

References in the text should be (Smith 1999), without a comma, or Smith (1999). Two articles by a single author should be (Smith 1999a, 1999b) or Smith (1999a, 1999b). For papers in press, use "in press", not the expected publication date. The Literature Cited section should include all papers referred to in the paper. Journal names should be spelled out completely and in italics.

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